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A MONOGRAPH OF *SABAL* (ARECACEAE: CORYPHOIDEAE)

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ABSTRACT

This monographic study of the New World genus *Sabal* (Arecaceae: Coryphoideae) recognizes 15 species. In addition to defining species limits and distributions, the study addresses broader questions concerning likely modes of speciation in the group and biogeographic radiation. The systematic treatment incorporates results from extensive field work and studies of leaf anatomy and flavonoid phytochemistry, ecology and biogeography, and morphology. Distribution maps and a key to the taxa are provided. Solutions are offered for the many nomenclatural problems that existed in the genus. A phylogenetic hypothesis, the first for the genus, is proposed. Moreover, phytochemical and anatomical features are examined in an ecological perspective, and hypotheses about their function and evolutionary significance are presented.

Key words: anatomy, Arecaceae, Caribbean, Mexico, morphology, Palmae, phytochemistry, *Sabal*.

INTRODUCTION

One of the most common genera of palms in and around the Caribbean basin is the genus *Sabal* (Arecaceae: Coryphoideae). It is widespread and often weedy, thriving in anthropogenic habitats from Bermuda to Sonora, from Texas to Trinidad. Likewise, it is common in the southeastern United States and is likely one of the palms best known to north temperate botanists. *Sabal* is widely cultivated as an ornamental in gardens around the world; in its native habitats, it sustains thatch, basketry, and hat-making industries. Yet despite its familiarity, *Sabal* has remained poorly studied and poorly understood.

Previous workers (Bailey 1934, 1944; Beccari 1907) confined their efforts to morphological taxonomic studies of genus. Faced with the general morphological sameness of the species and confounded by inadequate collections, they were most concerned with defining species boundaries. *Sabal,* the sole member of the subtribe Sabalinae of the tribe Corypheae (Uhl and Dransfield 1987), was clearly circumscribed at the genus level, but species boundaries were ill-defined. At the root of much of the past taxonomic confusion lay narrow species concepts in which nearly every separate population was recognized as a distinct species. Only with an appreciation for the ease with which *Sabal* has dispersed over long distances do we begin to develop a meaningful species concept for this group.

The present monograph has incorporated morphological, anatomical, and phytochemical data in an evolutionary and ecological framework. In addition to a key to the taxa, distribution maps, species descriptions and full synonymies, a phylogenetic hypothesis is provided. It is the first phylogeny proposed for the genus. Three additional questions are addressed: What has been the likely mode of speciation in the group? What can the phylogenetic hypothesis and present day distribution reveal about past biogeographical events and patterns? What adaptations are present in *Sabal* that allow it to succeed so well in a variety of environments in and around the Caribbean?

Distribution and Ecology

The distribution of *Sabal* is primarily Mexican, southeastern United States, and Caribbean (including Bermuda), with an outlying species found in Costa Rica, Panama, Venezuela, Colombia, and Trinidad (Fig. 1). Several disjunctions in the distribution are immediately apparent.

Sabal mauritiiformis is known from southern Mexico, southeastern Costa Rica, eastern Panama and the adjacent northern coast of South America. It is also found in southern Trinidad and has been reported by Wessels Boer (1988) from the islands of Curaçao and Bonaire. Its present distribution is probably recent, since it grows in lowland wet tropical forests that were submerged until quite recently.

Four other disjunctions are also readily attributable to overwater dispersal of seeds: those of *S. maritima, S. palmetto, S. causiarum,* and *S. yapa. Sabal maritima* is found on both Cuba and Jamaica (and is the only species of *Sabal* on Jamaica). Its present distribution—on recent soils on both islands—may also be recent, or it may have moved into these soils as other soils on the islands weathered. *Sabal causiarum* is found on Hispaniola and Puerto Rico; it inhabits lowland disturbed areas on both islands. *Sabal palmetto* is found in Cuba, the Bahamas, and the southeastern United States; *S. yapa* occurs on the Yucatán Peninsula (in Mexico and Belize) and western Cuba.

Island endemism is common in the genus, with one quarter of the species endemic to the Greater Antilles and Bermuda. Two species of Florida, *S. etonia* and *S. miamiensis,* are endemic to islandlike areas, the Central Florida Ridge and the Everglades Keys, respectively.

Most widespread species of *Sabal* (*S. mauritiiformis, S. mexicana, S. palmetto,* and *S. yapa*) as well as island endemics (*S. causiarum, S. domingensis,* and *S. maritima*) are small-fruited trees of the forest canopy. They thrive in high light intensity environments and commonly persist after forests are cleared for agricultural purposes. Recruitment in *S. palmetto* is a case in point. The species grows readily in oak forests in northern Florida, but seedlings under a closed canopy remain suppressed and form no aboveground stem. Stem elongation and sexual maturation await gap formation in the canopy. Along forest margins, on dunes, and in fields, growth and recruitment are immediate with no suppressed stage.

These species, as well as *S. bermudana, S. rosei,* and *S. pumos,* are "weedy" species, colonizing gaps and patchy habitats. They withstand burning and thrive in anthropogenic habitats. *Sabal uresana,* a species of xerophyllous woodlands of northwestern Mexico, appears to survive less well in disturbed habitats and, as noted by Gentry (1942), appears to be declining in the wild. This species never forms large stands in cleared fields as do its congeners *S. rosei* and *S. pumos.*

Sabal minor is an understory species of deciduous forests, while *S. etonia* and *S. miamiensis* are understory species of pine-oak associations in Florida.

MATERIALS AND METHODS

Field Studies

In the years 1984–86, I studied 13 populations of species occurring in Florida in the field. During the summers of 1986 and 1987, natural populations and cultivated individuals of *Sabal* were studied throughout Mexico. In 1988, field studies were undertaken in Panama, Cuba, Bermuda, the Dominican Republic, Trinidad, and Jamaica, as well as in southern Florida.

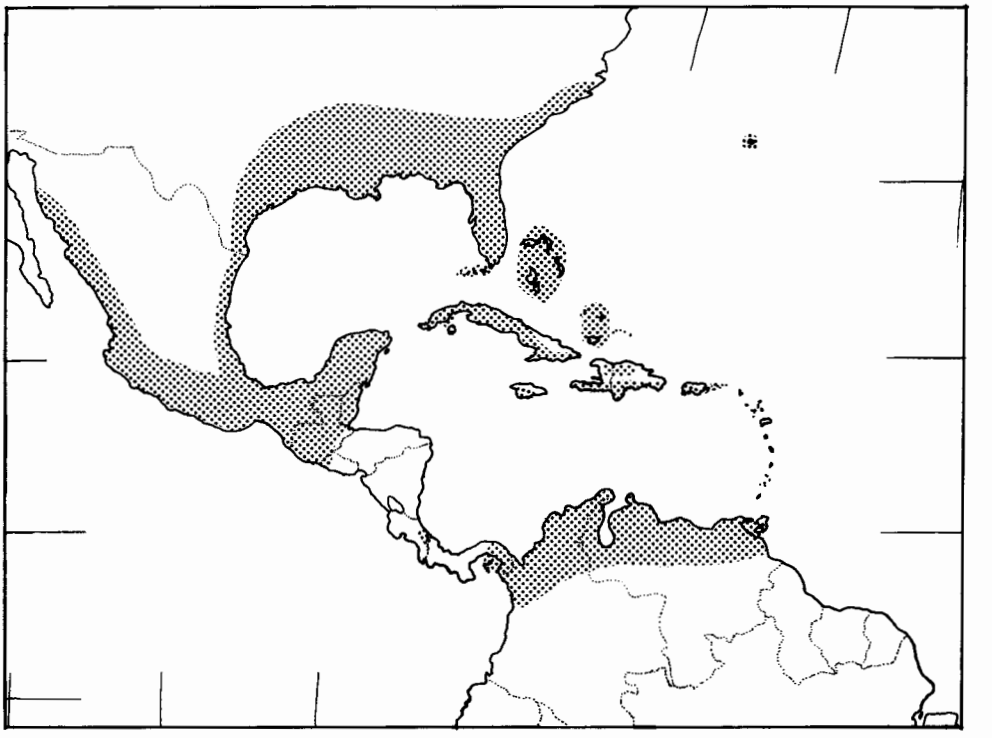

Fig. 1. Distribution of *Sabal*, a strictly New World genus.

At each population, complete voucher specimens were gathered and a separate collection number was given to each individual collected. Specimens collected prior to September, 1985, are deposited at FLAS, with duplicates distributed to various herbaria. Specimens collected after September, 1985, are deposited at RSA, with duplicates to be distributed.

Field observations of characteristics not readily visible from dried specimens include: species abundance, altitude, soil type, associated species and vegetation type, trunk height, diameter and surface texture, leaf number and color, petiole length, inflorescence number, length and posture, flower color and fragrance, insect visitors, fruit color, seed dispersers, and seed predators.

In addition, collections of flowers, fruits, and leaf samples were preserved in FAA and later transferred to glycerine-alcohol (Martens and Uhl 1980). These specimens were used for anatomical and morphological investigations. Dried bulk samples of leaf material were collected for phytochemical analysis. Living seed, when available, was collected and distributed to the Seed Bank of the International Palm Society, Fairchild Tropical Garden (Miami, Florida), Huntington Botanical Garden (San Marino, California), and Jardín Botánico (Mexico City, Mexico).

Herbarium Studies

Over 500 herbarium specimens were examined in the course of this study. Four herbaria (BH, FI, MEXU, P) were visited, and numerous herbaria (see Acknowledgments) lent material for study. Study of herbarium material was essential not

only for determining the range of morphological variation but also for compiling data on geographic and altitudinal distribution and common names.

Bailey (1934, 1940, 1944) has written eloquently and often on the problem of preparing specimens of *Sabal* for the herbarium. The large stiff leaves and inflorescences resist the press and demand special techniques. I have found the following method of preparation and storage to be suitable for *Sabal*: a healthy leaf is selected and removed from the tree, the petiole below the hastula is measured and then discarded (petiole length varies according to shade received), one half of the lamina is cut away taking care not to cut the hastula, and the outermost segments of the other half of the lamina (often wind-torn and the first segments to senesce) are trimmed away. Once trimmed in this fashion the leaf specimen is folded to fit the herbarium case, held in place with rubber bands, placed in a press, and dried. The inflorescence (or infructescence) is likewise trimmed of half its branches, and only the lower one or two primary branches (and all of their branches) are preserved. The inflorescence specimen is folded, held in place with rubber bands, and pressed. Specimens prepared in this fashion are bulky and are usually stored in boxes, but they have that advantage in that they can be unfolded and examined from all sides, unlike sheet-mounted specimens.

Methods for Measurement of Specimens

Measurements were taken from both living or pickled material and dried pressed specimens. Measurements of floral parts were made from herbarium specimens rehydrated by boiling. Measurements of large structures were made with either a metric scale measuring tape or ruler, and those of small structures were made with rotary dial micrometer (SPI 31-414).

Tree height was estimated visually; trunk diameter was measured on living specimens. Petiole and blade lengths were measured at the time of collection prior to pressing. All other vegetative measurements were taken from dried specimens. Petiole width was measured at the juncture of the petiole and hastula. Leaf segment measurements were taken from a segment midway along one side of the hastula. Segment width and lamina thickness were taken immediately above (distal to) the point of segment connation. Only one set of measurements was made for each collection.

Inflorescence length was either estimated visually or measured at the time of collection. Its natural position relative to the leaves was recorded. Rachilla diameter and length and bracteole length were taken from pressed specimens; all other floral measurements were made from rehydrated flowers. Rachillae length and number were measured (one for each collection) from basal branchlets (penultimate branches), and thus represent maxima for these characters; rachillae tend to be shorter and fewer in number on terminal penultimate branches. Rachilla thickness was taken midway along a rachilla from a middle rachilla; for both thickness and length, in no case was a terminal rachilla used. Petals, because their margins are involute, were measured at their widest points by folding them transversely, thus inducing their margins to unroll. Only one set of floral measurements was made for each collection.

Fruits and seeds were measured in the dry condition. From each collection, five fruits and seeds, selected at random, were measured, tabulated, and averaged; every effort was made to include only mature fruits and seeds.

MORPHOLOGY

Stem and Root

Stem formation begins underground in *Sabal.* A germinating seedling shows a peculiar geotrophic behavior, forcing the plumule downward. The eophyll emerges from the upturned tip of the plumule through a short series of tubular bracts (actually bladeless eophylls). The germination mode is remote and is figured by Bailey (1944, fig. 189). Aerial stem formation does not commence until many years' growth underground. In species that typically have no aerial stem, such as *S. etonia,* continued stem formation underground results in the curiously twisted or sigmoid underground stem illustrated by Bailey (1934, fig. 147; 1944, fig. 192). The underground stem allows *Sabal* to withstand disturbance (viz., fire) and is a key factor in the ability of *Sabal* to colonize open areas.

The aerial trunk of *Sabal* ranges from 3 m (in some populations of *S. minor*) to 25 m tall. Most caulescent species are 5–15 m tall. Trunk diameter can range from 15 cm (*S. yapa*) to 60 cm (*S. causiarum*), with most species falling in the 35–45 cm range. The surface of the trunk (when not clothed in persistent leafbases) may be smooth and white-gray or rough, vertically fissured, and gray-brown. In *S. pumos* and *S. rosei,* peg-like remains of petioles may persist on the trunk. The trunk may be green early in the life of the palm, and some species (*S. yapa, S. bermudana*) have nodal rings clearly to obscurely visible.

Aerial stem formation is an unreliable taxonomic character and has been the source of much taxonomic confusion in the past. The presence of an aerial stem was used by Cook (1901) to segregate the genus *Inodes* from *Sabal,* and several names have been proposed for populations of *S. minor* with aerial stems. Species that typically form large aerial stems can sometimes achieve reproductive maturity prior to aerial stem formation. This behavior is known in *S. mexicana, S. palmetto,* and *S. yapa.*

Roots of *Sabal* are large, numerous, and arise adventitiously along the stem. They arise uniformly around the base of aerial stems, but may arise only on the lower surface of sigmoid underground stems (see Bailey 1944, fig. 192).

Leaf

Petioles are 30–250 cm long, the length often depending on the amount of shade received and hence the amount of etiolation. Petioles are always unarmed in *Sabal.* The petiole is convex abaxially, but the adaxial side is concave or channeled, with a ridge formed in the channel of the distal half of the petiole.

Specific distinctions based on the presence or absence of persistent leafbases have no validity. Upon senescence, a leaf typically breaks off midway along the petiole; the petiole stub may persist (sometimes retaining photosynthetic ability) or abscise. The petiole sheathes the stem for a short distance, and as the stem expands, the persistent petiole base splits longitudinally forming a characteristic crisscross pattern (Fig. 30). Over time, the remains of the petiole base fall or rot away, but while present, they provide a foothold for epiphytes and hemiepiphytes, as well as a home for insects and other small animals.

The petiole is inserted into the blade at the hastula (Fig. 2A). The hastula forms on the adaxial surface in *Sabal* and may be short and obtuse or long and acuminate. It is usually asymmetrical in that one side is longer than the other. The margin

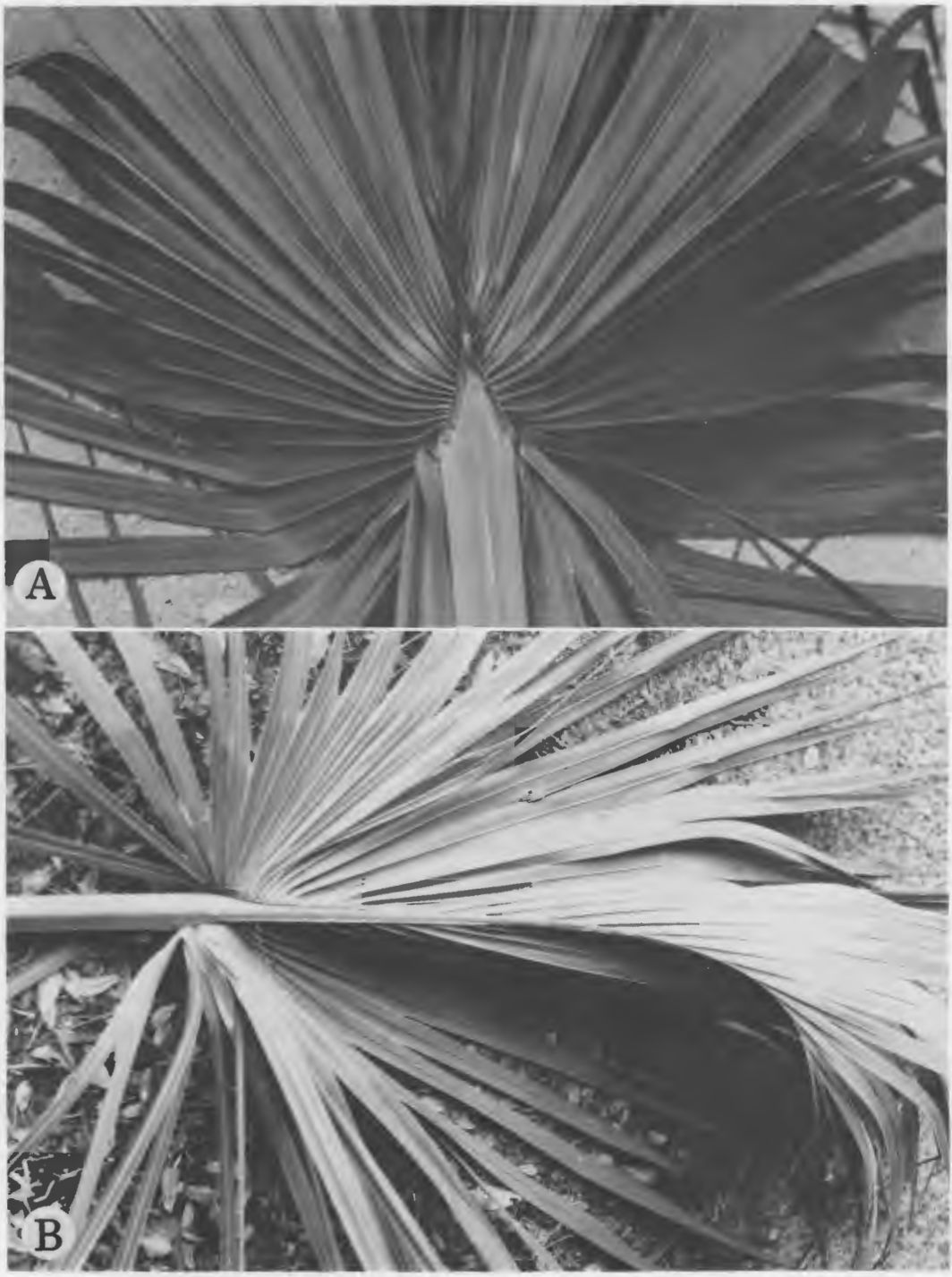

Fig. 2. Leaf morphology in *Sabal* (*S. palmetto*).—A. Adaxial surface showing hastula at apex of petiole.—B. Abaxial surface showing the costa, the extension of the petiole into the blade.

of the hastula may be entire or undulate, erect, involute, or revolute. The size and shape of the hastula are useful taxonomically only in the most general way (Moore 1971*a*).

In some populations of some species (viz., *S. mexicana* in Veracruz, Mexico, and *S. mauritiiformis* in Trinidad) the hastula is highly involute, so much so that the adaxial surface of the hastula is no longer visible. The curled abaxial edge of the hastula may bear the impressions of the underlying leaf segments giving the hastula a ridged appearance.

The leaves of *Sabal* are alternate and spirally arranged, flabelliform, composed of 15–120 segments (in the range of 60–75 for most species), and weakly to strongly costapalmate. The costa in a strongly costapalmate species typically curves downward (Fig. 2B), giving the leaf its characteristic rigid curvature. Segments are induplicate with a strong central vein, the midvein, and along their margins of connation, a strong suture vein is formed. Segments may be lax or rigid, bifid at the apex or not. Filamentous fiber extensions may be inserted between the segments (at the termination of the suture vein) and at the termination of the midvein in bifid segments. The leaves of *Sabal* may be glaucous or evenly green.

Segments are short (less than 100 cm) in some species (*S. etonia, S. minor*) or long (up to 200 cm), and the apical bifurcation may be shallow, deep, or absent. Lamina thickness ranges from less than 0.1 mm (in some species) to 0.5 mm. Segments may be connate for 15–50% of their length, with the least amount of connation among the outermost segments and the greatest among the terminal segments (those adjacent to the costa). The size of the palman (the proximal fused laminar portion of the leaf) shows some variation both within and among species.

In some species, leaf segments are grouped in twos or threes, with connation within groups nearly complete and connation between groups very slight. In *S. mauritiiformis,* splitting between segment groups occurs along a midvein, giving some segments a reduplicate appearance. This phenomenon is also known to occur in *Licuala* Thunb. (Corner 1966) and other coryphoid palms (Uhl and Dransfield 1987).

Peltate, multiseriate trichomes are present on young leaves of all species. They are brown with a laciniate margin and give young leaves a scurfy vesture. Usually, they are rapidly caducous. The trichomes persist longest along the abaxial side of the midveins. Only *S. maritima* frequently retains its trichomes for the life of the leaf.

Inflorescence

The paniculate inflorescence in *Sabal* is interfoliar, and its posture early in development and degree of ramification are diagnostic for some species (Fig. 3). The inflorescence may be erect (emerging 90° from horizontal), ascending (emerging less than 90° but greater than 45° from horizontal), arching (emerging ca. 45° from horizontal and arching downward), or cernuous (emerging more or less horizontally and hanging downward). Normally, ascending or arching inflorescences may sag under the weight of developing fruits, so inflorescence posture is best observed early in the development of the inflorescence before the rachillae have fully emerged. The inflorescence ranges in length from 0.4 to 3 m, and it is sparingly to densely branched. There are 2–4 orders of branching enumerated according to the system of Tomlinson and Zimmermann (1968). The inflorescence

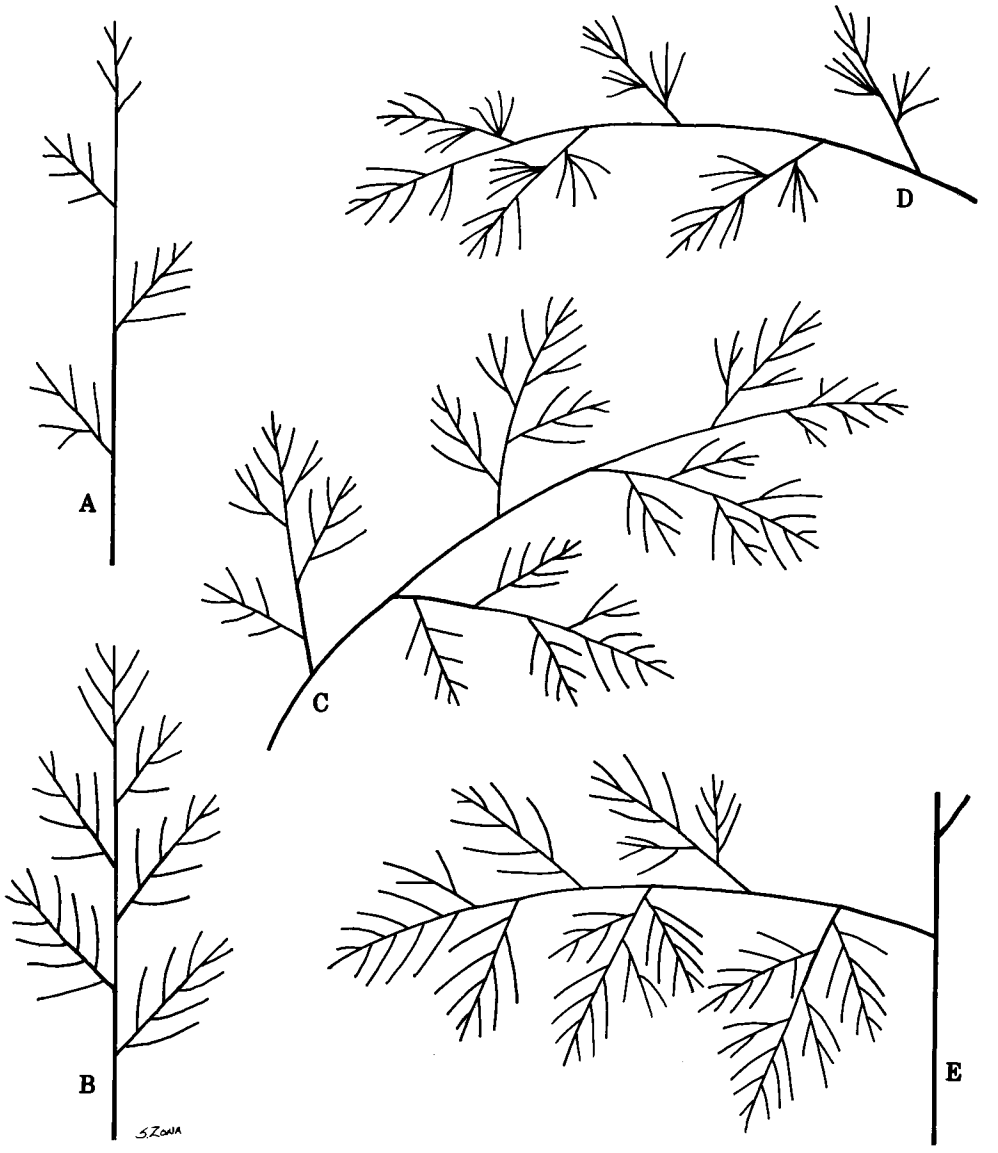

Fig. 3. Schematic diagrams of inflorescence branching patterns in *Sabal.*—A. *S. minor.*—B. *S. etonia.*—C. *S. causiarum.*—D. *S. bermudana.*—E. *S. mauritiiformis.*

is clasped by a sheathing bicarinate prophyll and 2–5 tubular bracts, according to the vigor of the plant. Branches up to and including the penultimate branches are each subtended by a bicarinate bract. Tubular bracts, with straight or oblique openings, clasp all branches up to and including the antepenultimate branches. The bicarinate bract of the penultimate branches may be exserted or inserted within the tubular bracts of the antepenultimate branches. The ultimate branches (the rachillae) are borne in the axils of solitary small triangular bracts. Flowers are subtended by one small bract, and a pedicillar bracteole is borne obscurely on each flower (Morrow 1965).

Rachillae are more or less terete to strongly angular in cross section, and although rachilla shape has been taken as a specific character by Beccari (1907) and Bailey (1944), it has no taxonomic value over a broad range of collections. A rachilla gradually tapers from its base to its apex; however pathogenic conditions (fungal in origin?) may give rachillae a puffy or swollen appearance. Swollen and fusiform rachillae have been mistaken as a characteristic of some species (e.g., *S. uresana*). Various fungal infections manifest by patches of hyphae and/or reproductive structures are commonly seen on rachillae of all species of *Sabal*.

Flower

Flowers of *Sabal* are borne singly. They are exposed in bud and open more or less acropetally along the inflorescence. Flower color is creamy white, and the flowers have a pungent sweet fragrance. They are ca. 3.5–7 mm high. Valuable taxonomic characters can been found in the flowers of some species (Fig. 4A), but there is generally a monotonous sameness to the flower morphology (Fig. 4B, C).

The calyx is carnose at the base, usually becoming membranous and hyaline at the apex. The calyx is typically costate when dry, although in *S. yapa,* which has a more carnose calyx, the costae are not apparent. The calyx may be cupulate (sides more or less parallel), campanulate, or urceolate.

Petals are generally membranous with hyaline and denticulate margins and are obovate to more nearly spatulate. In *S. yapa,* the petals are triangular-ovate and basally connate. They are generally noncostate when dry, but *S. mexicana* is noteworthy for its costate petals. A pattern of papillate cells is often visible on the adaxial surface of the petals (Fig. 4A). It resembles the letter "W" in parentheses, with the base of the "W" pointing toward the base of the petal. This (W) pattern is sometimes only weakly apparent, and its presence varies from individual to individual. The pattern may play a role in pollination ecology.

Stamens are in two whorls of three, connate basally, and adnate to the petals. The filaments are generally long triangular in shape (but acuminate in *S. yapa,* Fig. 4A). Typically, the stamens are ascending to spreading, with the filaments weakly sigmoid, but in some species the antipetalous stamens are reflexed, and the antisepalous stamens are ascending to erect (Fig. 4C). Anthers, twice as long as they are wide, are yellow, versatile, and dehisce latrorsely. Pollen in *Sabal* possesses an elliptical amb and a finely reticulate exine. It is uniform throughout the genus and has no apparent taxonomic value (Sowunmi 1972).

Gynoecia are composed of three fused carpels and are variously shaped: conical, pyriform, or lageniform. Gynoecia are of little taxonomic value, as their size and shape varies considerably among individuals. The stigma is obscurely three lobed and papillate. It is rounded or truncate and about 0.5 mm in diameter.

Fruit and Seed

Fruits of *Sabal* are usually single-seeded berries. Occasionally, more than one ovule matures, and two- or three-lobed berries result. Fruits are spherical, oblate, or pyriform, with the style and stigmatic remains persisting basally along with the calyx and, more rarely, the perianth. Fruits range in size from 6.5 to 27.5 mm in diameter and from 6.5 to 22.5 in height. Fruits are green when immature,

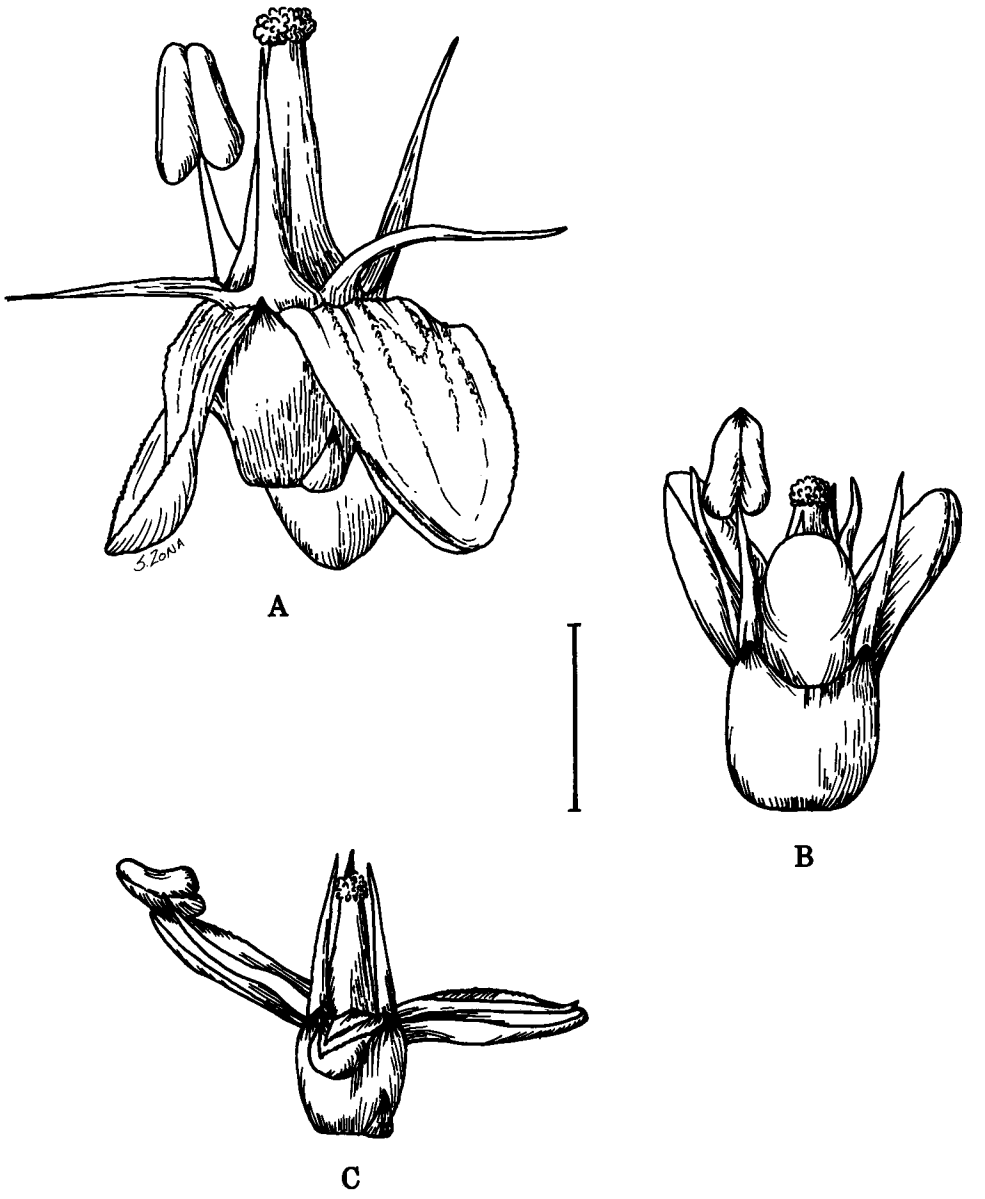

Fig. 4. Flowers of *Sabal* (all but one anther removed from each).—A. *S. yapa* (from *Marie-Victorin 58168*).—B. *S. maritima* (from *Zona 279*).—C. *S. mauritiiformis* (from *Zona et al. 264*). (Scale = 2 mm.)

passing through a brownish stage, eventually becoming black in most species; in some species, however, fruits are dispersed while still in the greenish brown stage.

The epicarp is smooth and thin; the mesocarp is thick and sweet in most species but may be thin and dry in *S. minor*. The endocarp is dry and membranous and shiny brown, separating easily from the seed.

The seed is oblate-spherical and brown to black. The seed is concave on the funicular end, but the depression may be more or less filled with the funicular

remains. Seeds are 4.5–18.8 mm in diameter by 4.0–11.2 mm in height. The testa is smooth and shiny, but immature seeds, when dry, take on a rugose appearance that has been mistaken to have taxonomic significance in *S. uresana.* The embryo is small (<2.0 mm in length) and poorly developed at the time of seed dispersal. The embryo position is betrayed by a small ringlike depression in the testa. The embryo may be located equatorially to supraequatorially. Very rarely, individuals may be found to possess seeds with subequatorial embryos. Beccari (1907) attached considerable significance to embryo position, but over a large sample size, meaningless variation in this character state is readily apparent. The endosperm is bony, white, and homogeneous.

LEAF ANATOMY

Introduction

Palms have been the subject of much attention from plant anatomists; although this attention has most often been directed to fundamental problems of xylem or phloem transport (Tomlinson and Zimmermann 1965, 1966; Parthasarathy and Tomlinson 1967), development of the plicate leaf (Kaplan, Denger, and Denger 1982), or derivation of the diverse inflorescence structures within the family (Uhl and Moore 1978). The application of anatomical data to systematic problems in the palm family has most often been at the genus level or above (Tomlinson 1961). Several workers (Barfod 1988; Glassman 1972*b*; Read 1975; Uhl 1972, 1978*a, b*) have demonstrated the value of anatomical data at the species level, and of course for palm palaeobotanists (Daghlian 1978; Dilcher 1971), anatomy is their stock in trade.

Relatively little anatomical work has been interpreted in an ecological light. Uhl and Moore (1977), who discussed floral anatomy and pollination, and Barfod (1988), who described leaf anatomy, both drew correlations with ecology.

Sabal has received little attention from comparative anatomists. Limited ethnobotanical data (E. Sandoval pers. com.) suggested that differences in usefulness of the species for thatch and basketry may reflect differences in their anatomy. The abundance of sterile specimens and great ecological diversity suggested that leaf anatomical studies could produce useful taxonomic, ethnobotanical, and evolutionary information.

Materials and Methods

Transverse sections were prepared for anatomical study following the methods outlined in Martens and Uhl (1980). Although numerous collections were examined (Appendix 1), quantitative data from only one specimen per species are presented in Table 1. Collection data are abbreviated in Table 1; complete data for each specimen may be found in the taxonomic treatment. Leaves were sampled from the middle segment (of one side of the leaf) at or near where the segments become free. Pickled or rehydrated lamina samples, including the midvein, were desilicified in HF, dehydrated in an alcohol series, embedded in paraffin, and sectioned at 12–14 μm on a rotary microtome. Sections were stained with a standard safranin-fast green combination and mounted in a synthetic resin (Permount).

Lamina samples were cleared using 2.5% NaOH at 60 C for 12–24 h, then bleached with one-third strength commercial bleach for 5–10 min. Cleared sam-

Table 1. Anatomical features of *Sabal*.

1	2	3	4	5	6	7	8	9	10
S. bermudana (*Zona 283*)	356 ± 8	+; 16	=	3–7	9 ± 2*	8 ± 1	11 ± 2*	12 ± 2	84 ± 15
S. causiarum (*Bailey 18*)	360 ± 20	−; 11	≠	7	8 ± 1*	7 ± 1	11 ± 2	11 ± 2	69 ± 16
S. domingensis (*Bailey 238*)	404 ± 12	+; 19	≠	14	9 ± 2*	6 ± 2	9 ± 2	9 ± 2	99 ± 25
S. etonia (*Thorne 57944*)	331 ± 26	+; 17	=	3	10 ± 2*	9 ± 2	14 ± 2*	13 ± 2	55 ± 12
S. guatemalensis (*Moore 8209*)	418 ± 22	−; 9	≠	7+	6 ± 1	7 ± 1	10 ± 2	10 ± 2	89 ± 23
S. maritima (*Zona 301*)	415 ± 18	+; 16	≠	7	7 ± 1	6 ± 1	10 ± 2*	11 ± 2	95 ± 29
S. mauritiiformis (*Zona 141*)	207 ± 16	−; 9	≠	7	12 ± 1*	10 ± 2	—	10 ± 2	37 ± 10
S. mexicana (*Zona 221*)	471 ± 24	−; 12	≠	3–7	9 ± 2	10 ± 2	14 ± 2*	12 ± 2	89 ± 23
S. miamiensis (*Small & Nash s.n.*)	307 ± 15	+; 20	=	3	6 ± 1	6 ± 1	9 ± 1	9 ± 2	67 ± 14
S. minor (*Perkins 987*)	240 ± 25	+; 15	=	1	5 ± 1*	4 ± 1	9 ± 2	10 ± 2	49 ±16
S. palmetto (*Zona 158*)	367 ± 17	+; 19	=	3	5 ± 1	6 ± 1	9 ± 3	8 ± 1	79 ± 12
S. pumos (*Zona 250*)	326 ± 14	+; 28	=	1–3	7 ± 1*	5 ± 1	8 ± 1	8 ± 1	48 ± 14
S. rosei (*Zona 248*)	364 ± 21	+; 16	=	3	7 ± 1*	6 ± 1	8 ± 1*	7 ± 1	69 ± 12
S. uresana (*Zona 257*)	498 ± 21	+; 16	=	3–7	13 ± 1*	11 ± 2	17 ± 3	18 ± 3	94 ± 16
S. yapa (*Zona 144*)	337 ± 41	−; 22	=	3	10 ± 2*	8 ± 2	14 ± 3*	12 ± 1	54 ± 16

1. Taxon and voucher specimen. 2. Lamina thickness (μm), mean of 25 measurements ± one standard deviation. 3. Bundle sheath extensions, present (+) or absent (−); number of BSE's or larger vascular bundles between midvein and suture vein. 4. Adaxial and abaxial palisade layers equal (=) or unequal (≠) in thickness. 5. Number of adaxial small vascular bundles between large vascular bundles or BSE's. 6. Adaxial cuticle thickness (μm), mean of 25 measurements ± one s.d. Asterisk indicates significant difference between adaxial and abaxial means (Student's t-test). 7. Abaxial cuticle thickness (μm), mean of 25 measurements ± one s.d. 8. Adaxial stomata depth (μm), mean of 25 measurements ± one s.d. Asterisk indicates significant difference between adaxial and abaxial means (Student's t-test). 9. Abaxial stomata depth (μm), mean of 25 measurements ± one s.d. 10. Abaxial fiber bundle height (μm), mean of 25 measurements ± one s.d. 11. Bundle sheath or large vascular bundle vessel inside diameter (μm), mean of 25 measurements ± one s.d. 12. Mean number of wide vessels per bundle. 13. Transverse commissures short and straight (S) or long-looping (L); running through the middle of the mesophyll (M) or below the middle (B). 14. Midvein shape in cross section: trapezoidal (A), rectangular (B), or triangular (C). 15. Fiber distribution in expansion area of midvein: axillary (A), scattered (S), or absent (−). 16. Midvein vessel inside diameter (μm), mean of 25 measurements ± one s.d. 17. Number of bundles with wide vessels in midvein. 18. Tannin sac or deposit location: A = in mesophyll; B = in parenchyma of midvein; C = around BSE's or large vascular bundles; D = in epidermis; E = in hypodermis (especially at BSE's or vascular bundles); F = in bulliform cells of midvein expansion region; G = peripheral to expansion region; H = within fiber sheath of BSE's or large vascular bundles; I = around transverse commissures. Asterisk indicates faint or scattered presence.

Table 1. Continued.

1	11	12	13	14	15	16	17	18
S. bermudana (*Zona 283*)	47 ± 12	1.6	S/M	A	A	48 ± 16	5	C*, E*, H*
S. causiarum (*Bailey 18*)	57 ± 15	1.8	L/B	B	S	63 ± 16	9	A, H
S. domingensis (*Bailey 238*)	59 ± 15	1.6	L/B	A	S	82 ± 20	8	H, I
S. etonia (*Thorne 57944*)	30 ± 7	1.4	S/M	C	–	39 ± 8	3	A*, E, G, H, I
S. guatemalensis (*Moore 8209*)	62 ± 16	1.9	L/B	A	S	72 ± 22	7	A, B, F
S. maritima (*Zona 301*)	61 ± 10	1.7	L/B	C	S	55 ± 11	9	A, C, H, I
S. mauritiiformis (*Zona 141*)	29 ± 8	1.3	L/B	B	A	46 ± 10	2	A*
S. mexicana (*Zona 221*)	57 ± 10	1.7	L/B	B	S	57 ± 14	8	–
S. miamiensis (*Small & Nash s.n.*)	45 ± 8	1.8	S/M	A	–	47 ± 15	3	A, B, E, G, H, I
S. minor (*Perkins 987*)	25 ± 4	2.8	S/M	C	–	22 ± 4	2	A*, E*
S. palmetto (*Zona 158*)	53 ± 13	2.1	S/M	A	A	43 ± 17	6	A*, C, E, G*, H
S. pumos (*Zona 250*)	45 ± 9	1.4	S/M	B	A	43 ± 13	5	A, B
S. rosei (*Zona 248*)	63 ± 15	1.7	S/M	B	S	59 ± 22	9	A, B, C
S. uresana (*Zona 257*)	59 ± 16	3.4	S/M	B	S	58 ± 16	11	A, B, D, F
S. yapa (*Zona 144*)	41 ± 11	1.8	L/B	B	S	52 ± 11	4	–

ples were dehydrated in an alcohol series, stained with a mixture of safranin and fast green, then destained for approximately 2 h in absolute ethanol before being transferred to ethanol-xylene (1:1), and ultimately to xylene. Samples were mounted in synthetic resin.

Anatomical measurements were made with the aid of a digitizer. The slide image was projected onto the digitizing pad, and data were quantified with the software package SigmaScan, version 3.9 (Jandel Scientific, Corte Madera, California). Statistical analysis was possible within SigmaScan.

Results

The leaf of *Sabal* is generally isolateral, with cutinized epidermises, and with one exception, stomata on both surfaces. Trichomes are absent from the lamina but may be present near the hastula along the mid- and suture veins. Epidermal cells lack sinuous anticlinal walls. Stomata are restricted to the intercostal regions and are plugged by cutinous substances. Beneath each epidermis is a hypodermis one or two cell layers thick. The chlorenchyma is palisadelike beneath each surface and surrounds a mesophyll comprised of large spherical cells. Septate fibers in strands are attached to the abaxial hypodermis; although these are sometimes converted into small vascular bundles. Large vascular bundles, sometimes encased in bundle sheath extensions, are present; small vascular bundles, suspended from the adaxial hypodermis by fiber bands, are interspersed among the large vascular bundles. Large transfer cells are present around the middle of bundle sheath extensions, large vascular bundles, and small vascular bundles. Phloem is present in two to three separate strands, vessels are present in the metaxylem, and parenchyma is scattered within the vascular bundle. Transverse commissures are variable in abundance and distribution, but are always present. The midvein is composed of two to many vascular bundles, often encased in a single fiber sheath. Smaller fiber bundles are arrayed around the periphery of the midvein. On the adaxial side, there is a prominent region of bulliform cells, which function in the expansion of the leaf. The suture vein, the rib joining the margins of two leaf segments, is similar in all respects to the midvein, but is more highly variable throughout its length. Stegmata and raphides may be abundantly present throughout the leaf.

Lamina and midvein transections and leaf clearings of all species are illustrated in Figures 5–13. The results of the comparative study are summarized in Table 1. Both quantitative and qualitative data are presented. Differences in both reflect at least two selection pressures: changes in leaf size and adaptation to aridity. Closely allied to the latter selection factor is defense against herbivores. Each character given in Table 1 will be discussed with these evolutionary constraints in mind.

Discussion

Lamina thickness.—A clear trend in *Sabal* is toward thinner lamina in smaller leaves, but this trend is countered by the need for thicker leaves in more arid habitats. *Sabal minor* and *S. etonia* have the smallest leaves in the genus, but the leaves of the latter, a xerophytic species, are considerably thicker. *Sabal mauritiiformis* has large leaves overall, but the segments are clustered into groups of 2–

3, so structural support is modified, and the lamina is thin as if the leaf were small. *Sabal yapa* also has clustered leaf segments, but life in drier habitats has selected for medium thick leaves.

Bundle sheath extensions (BSE's).—Nearly all species have BSE's (Fig. 5A, D, 6A, D, E, 7A–D), and their presence is the unspecialized state within the genus. Six species (e.g., *S. yapa,* Fig. 7E) possess large veins sheathed by fibers, but the sheaths seldom extend from hypodermis to hypodermis. The lack of well developed BSE's is taken to have great phylogenetic importance.

The number of BSE's or large veins is also given for each species in Table 1. The range is from 18 to 56 per segment, with most species having 30–34. The evolutionary significance of either reduction or proliferation is unclear, as they appear to have no correlation with size (i.e., support) or drought adaptation.

Small adaxial vascular bundles (SVB's) between BSE's.—Generally, between a pair of BSE's, one finds three SVB's attached to the adaxial surface by a thick sheath of fibers. The central SVB is larger than the other two. Although one can easily imagine three as the "base number" on which reductions and elaborations in SVB number are made, outgroup comparison with *Washingtonia* and *Brahea* points to seven as the unspecialized state. Transformation of SVB's into BSE's produces the vasculature seen in *S. minor* (Fig. 6E), in which one SVB alternates with each BSE. In two species, *S. domingensis* (Fig. 5C) and *S. guatemalensis* (Fig. 5E), reduction of BSE's has led to more than seven SVB's between each BSE pair. In *S. bermudana, S. mexicana, S. pumos,* and *S. uresana,* the vasculature pattern is uneven within the leaf.

As with the preceding character, the functional or ecological significance of SVB number is not known.

Cuticle thickness—What is measured here is actually the cuticle together with the heavily cutinized outer wall of the epidermis. In those cases (indicated in Table 1) in which the adaxial cuticle differs in thickness from the abaxial cuticle, the adaxial cuticle is always thicker. This is a character which clearly shows ecological adaptation. Not unexpectedly, the species with the thickest cuticle is *S. uresana* (Fig. 7D) from the dry thorn scrub of Sonora.

Average stomatal depth.—Like the preceding character, this one shows ecological adaptations. For this character, the epidermis is measured from the upper lip of the guard cells to the surface of the leaf. If the average abaxial cuticle thickness is subtracted from the average stomata depth, one is left with the "true" depth of the guard cells below the epidermis. The data thus transformed, *S. uresana* (7 μm), followed by *S. minor* (6 μm) and *S. maritima* (5 μm), have the most sunken stomata. *Sabal minor* is a bit anomalous here in that it is not a palm of xeric or even seasonally dry areas. *Sabal mauritiiformis* and *S. rosei* have the shallowest abaxial stomata. If the adaxial data are similarly transformed, *S. mexicana* has the deepest stomata.

Fiber bundle height.—Fiber bundles attached to the abaxial hypodermis vary in height according to the size of the leaf and thickness of the lamina (Fig. 5–7). Although fiber bundles may play a role in herbivore defense, they are more likely acted upon by constraints in leaf size and lamina thickness. The broad overlap in range of values limits their systematic usefulness.

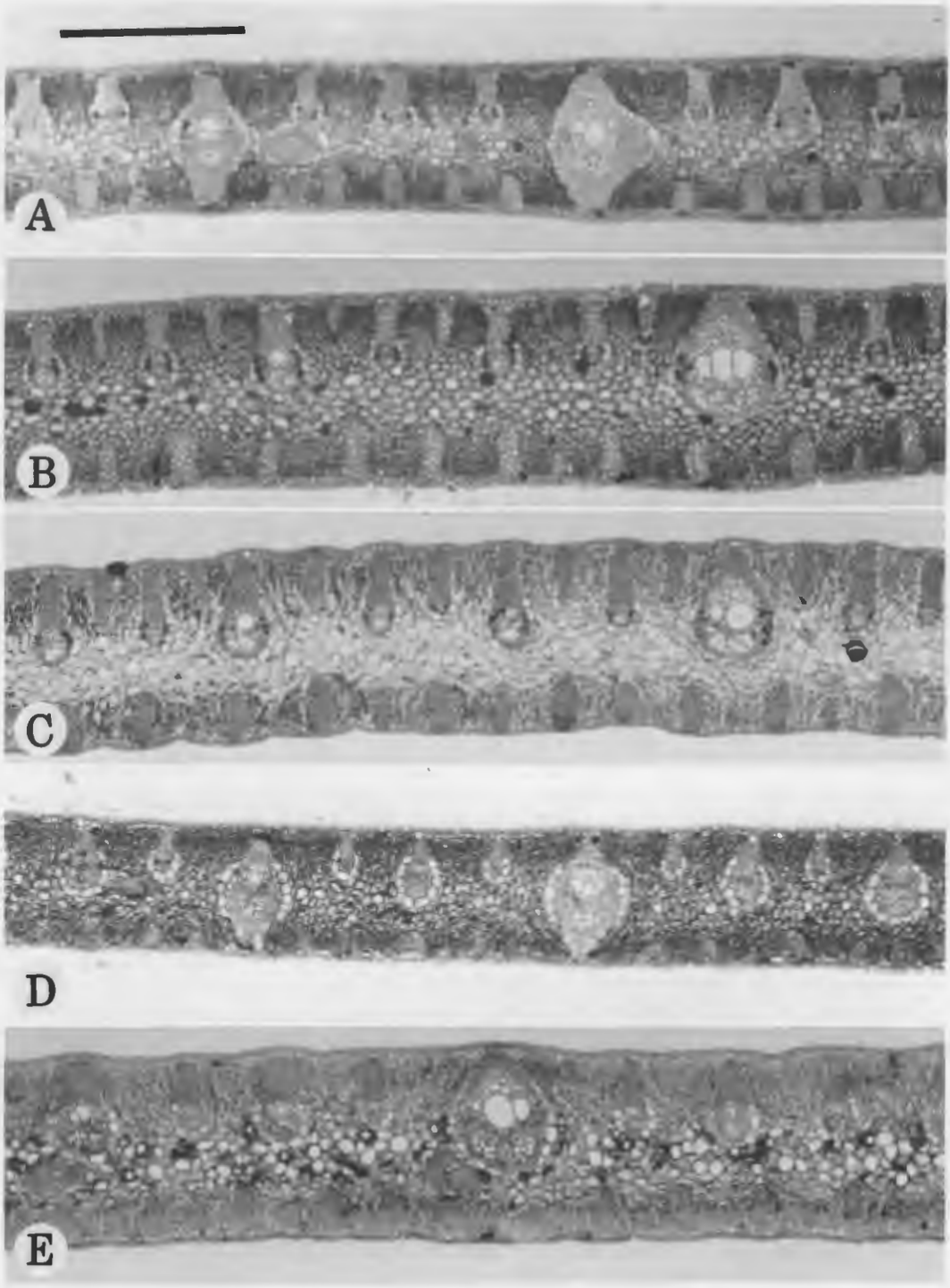

Fig. 5. Lamina transections of *Sabal*.—A. *S. bermudana* (*Zona 289*).—B. *S. causiarum* (*Zona et al. 293*).—C. *S. domingensis* (*Bailey 238*).—D. *S. etonia* (*Thorne & Judd 57944*).—E. *S. guatemalensis* (*Moore 8209*). (Scale in A = 0.4 mm.)

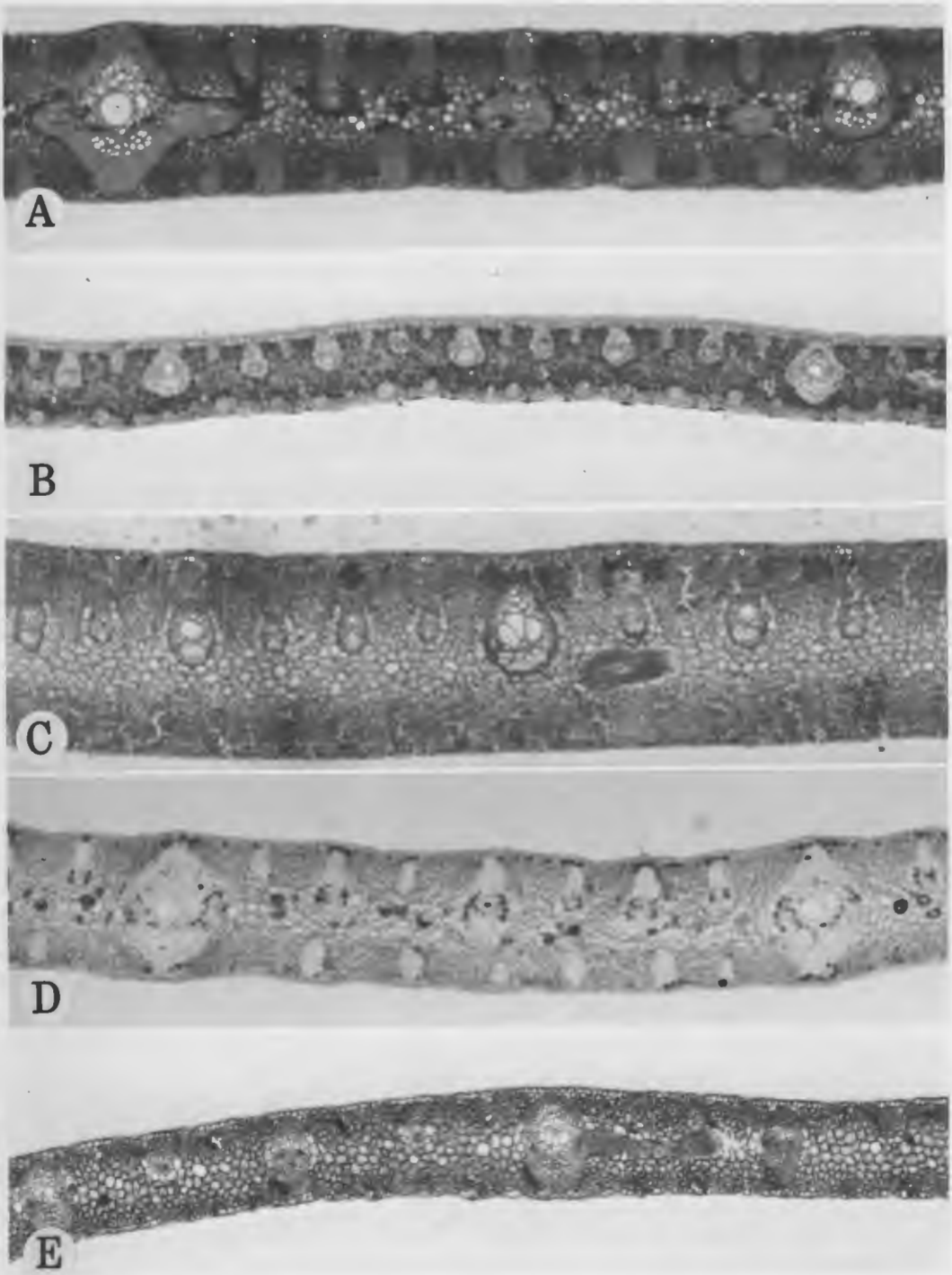

Fig. 6. Lamina transections of *Sabal*.—A. *S. maritima* (*Zona et al. 298*).—B. *S. mauritiiformis* (*Zona et al. 141*).—C. *S. mexicana* (*Zona et al. 221*).—D. *S. miamiensis* (*Small & Nash s.n.*).—E. *S. minor* (*Perkins & Herring 987*). (Scale as in Fig. 5A.)

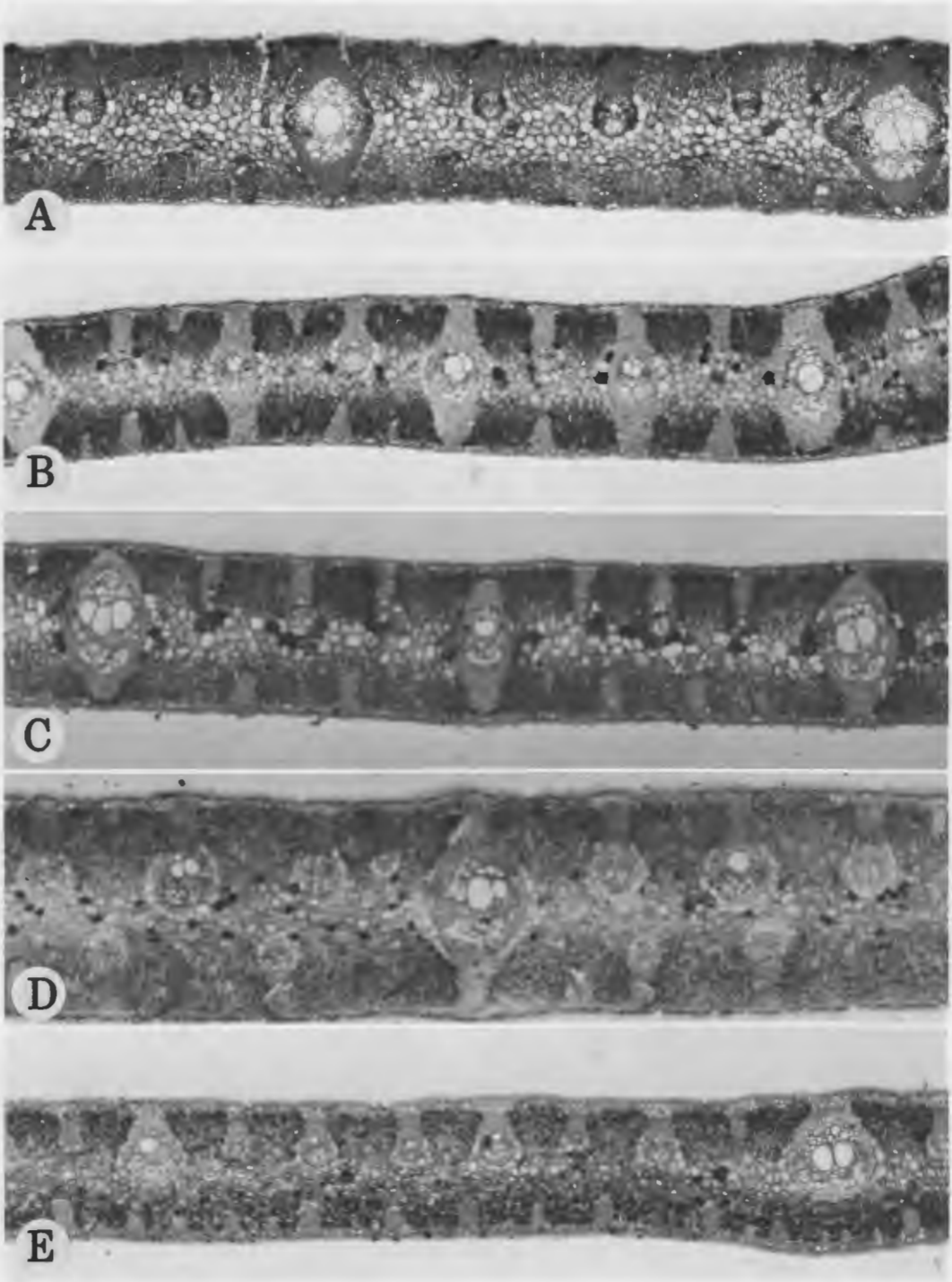

Fig. 7. Lamina transections of *Sabal*.—A. *S. palmetto* (*Zona 158*).—B. *S. pumos* (*Zona 250*).—C. *S. rosei* (*Zona et al. 240*).—D. *S. uresana* (*Zona et al. 257*).—E. *S. yapa* (*Zona et al. 144*). (Scale as in Fig. 5A.)

Large vessel diameter within BSE.—Width of the large vessels of the metaxylem is likely a characteristic under strong selection pressure. While large vessels are more efficient conductors of water, they are more susceptible to cavitation than narrow vessels. Lamina thickness is also an important constraint. *Sabal domingensis, S. guatemalensis, S. maritima, S. rosei, S. uresana,* and *S. yapa* have wider vessels than the remaining species. This group includes mesophytes (*S. guatemalensis* and *S. rosei*) as well as the most xerophytic species of the genus, *S. uresana.* Another xerophyte, *S. etonia* (Fig. 5d), has small vessels, similar in size to those of *S. minor* (Fig. 6e), a mesophyte. These results suggest that leaf size and vessel efficiency are stronger selection constraints than vessel safety.

Vessels per group within BSE.—Only three species are exceptional in having more than one wide metaxylem vessel per BSE bundle. They are *S. minor* (2.8 v/gr), *S. palmetto* (2.1 v/gr), and *S. uresana* (3.4 v/gr). In petiole vascular bundles, vessel number is known to have systematic significance at high taxonomic levels (Klotz 1978), and the Coryphoideae is the most variable in this character. Its ecological significance is not clear.

Palisade layers.—A leaf of *Sabal* does not posses a palisade layer in the traditional dicotyledonous sense of that word. Rather, there is both an upper (adaxial) and lower (abaxial) layer of compact, somewhat elongated chlorophyllous cells surrounding and intergrading with a mesophyll of larger (by a factor of 2–4) isodiametric cells. In no species of *Sabal* are the palisades clearly demarcated from the mesophyll; however, an important systematic feature is whether the palisades are equal in height (similar number of cell layers) or unequal in height (different number of cell layers). In *Sabal,* some species possess adaxial palisades that are 1.5 to 2 times as large as the abaxial palisades. These species are the Antillean species plus *S. mexicana, S. guatemalensis,* and *S. mauritiiformis.*

Transverse commissures (Fig. 8–9).—The pattern and distribution of transverse commissures in the leaves are very important systematic characters. In *Sabal,* patterns of transverse commissures tend to be either long-looping and prominent (as in *S. maritima,* Fig. 8F, or *S. yapa,* Fig. 9G) or short and straight and often obscure in the dry leaf (as in *S. etonia,* Fig. 8D, or *S. minor,* Fig. 9B). In addition, transverse commissures when long-looping tend to run below the middle of the mesophyll; short and straight transverse commissures tend to be found in the middle of the mesophyll. These two characters, while of uncertain ecological value, have great systematic importance and are not readily modified by environmental factors.

Midvein shape.—The shape of the midvein in transection, whether triangular, rectangular, or trapezoidal, is apparently correlated with leaf size. Species with small leaves most often have triangular midveins, and those with larger leaves have rectangular midveins. Medium size leaves have trapezoidal midveins. In this instance, structural support is the most important evolutionary constraint for *Sabal.*

Fiber bundle distribution.—The distribution pattern of fiber bundles within the expansion region is of systematic importance. Species with small leaves (*S. etonia,* Fig. 10D, *S. minor,* Fig. 11E, *S. miamiensis,* Fig. 12A) typically lack fibers altogether, a fact that suggests the fibers may play a major role in structural support

of larger leaves. In other species, the fibers are either scattered throughout the expansion region (as in *S. domingensis,* Fig. 10C) or arrayed along the axil of the fold, i.e., along the uppermost side of the midvein (as in *S. bermudana,* Fig. 10A).

Midvein vessel diameter.—The wide metaxylem vessels of the midvein show considerable variation in average diameter. Once again, diameter appears more closely correlated with leaf size than with constraints of ecology. It is of limited systematic importance, and its use in the phylogenetic analysis would be redundant.

Number of vascular bundles.—Between 2 and 11 vascular bundles containing wide metaxylem vessels are present in the midveins of *Sabal.* This character is strongly correlated with leaf size, or at least, functional size.

Tannin deposits.—There is great variation in the distribution and abundance of tannin deposits within the leaf (Fig. 5–7). These cells are often idioblastic and contain dark-staining substances, most likely procyanidin. They are present to varying degrees in the epidermis, hypodermis, mesophyll, around or within bundle sheath extensions, around transverse commissures, and/or around or in the bulliform cells of the midvein. There is great taxonomic and systematic value to the pattern of tannin deposits; although there is some intraspecific variation. Tannins are more readily observed in sections of fresh or pickled material than in sections made from old, dried collections.

Other cellular inclusions.—*Sabal* has both raphides and stegmata. The raphides are found in idioblastic cells in the mesophyll. Silica bodies (stegmata), roughly spherical and of varying sizes, are present in linear files along vascular bundles and/or transverse commissures (Fig. 9H). Undoubtedly, these inclusions arose as adaptations against herbivory; however, interpopulational variation has been observed in the abundance of both types of inclusions. These differences are thought to be random, and they probably do not reflect differences in herbivore pressure.

FLAVONOID CHEMISTRY

Introduction

Although palms are rich in flavonoids and other so-called secondary compounds (Bate-Smith 1962; Harborne, Williams, Greenham, and Moyna 1974; Williams, Harborne, and Clifford 1973), rarely has flavonoid chemistry been used at the

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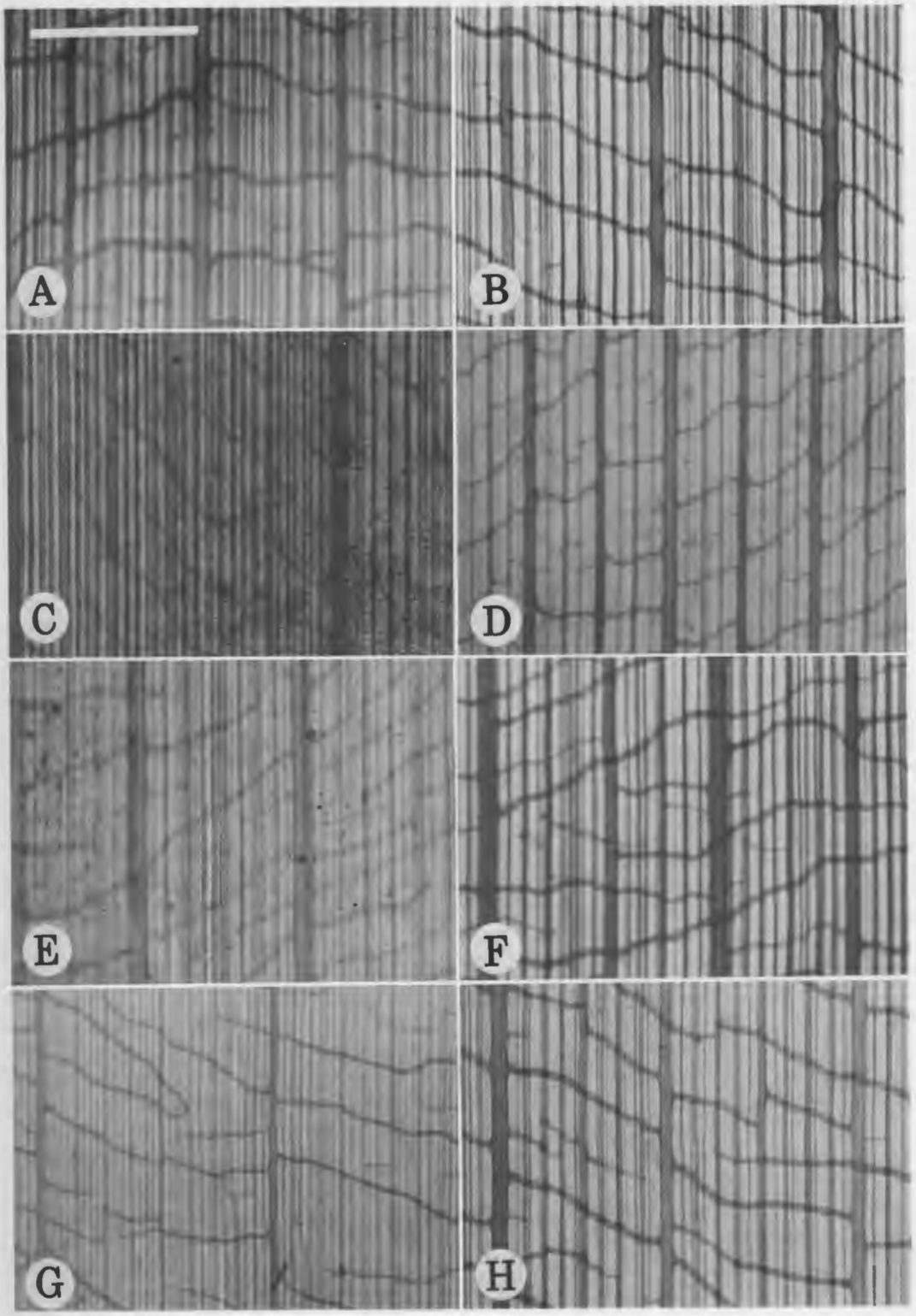
Fig. 8. Lamina clearings of *Sabal.*—A. *S. bermudana* (*Zona 283*).—B. *S. causiarum* (*Zona et al. 290*).—C. *S. domingensis* (*Bailey 238*).—D. *S. etonia* (*Thorne & Judd 57944*).—E. *S. guatemalensis* (*Moore 8209*).—F. *S. maritima* (*Zona et al. 299*).—G. *S. mauritiiformis* (*Zona et al. 141*).—H. *S. mexicana* (*Zona et al. 138*). (Scale in A = 2 mm.)

Fig. 9. Lamina clearings of *Sabal.*—A. *S. miamiensis* (*Small & Nash s.n.*).—B. *S. minor* (*Perkins & Herring 987*).—C. *S. palmetto* (*Zona 158*).—D. *S. pumos* (*Zona 250*).—E. *S. rosei* (*Zona et al. 248*).—F. *S. uresana* (*Zona et al. 257*).—G. *S. yapa* (*Zona et al. 144*).—H. Phase contrast to illustrate stegmata along veins (*S. causiarum, Questel 468*). (Scale as in Fig. 8A.)

Fig. 10. Midvein transections of *Sabal.*—A. *S. bermudana* (*Zona 289*).—B. *S. causiarum* (*Zona et al. 293*).—C. *S. domingensis* (*Bailey 238*).—D. *S. etonia* (*Thorne & Judd 57944*). (Scale in A = 0.4 mm.)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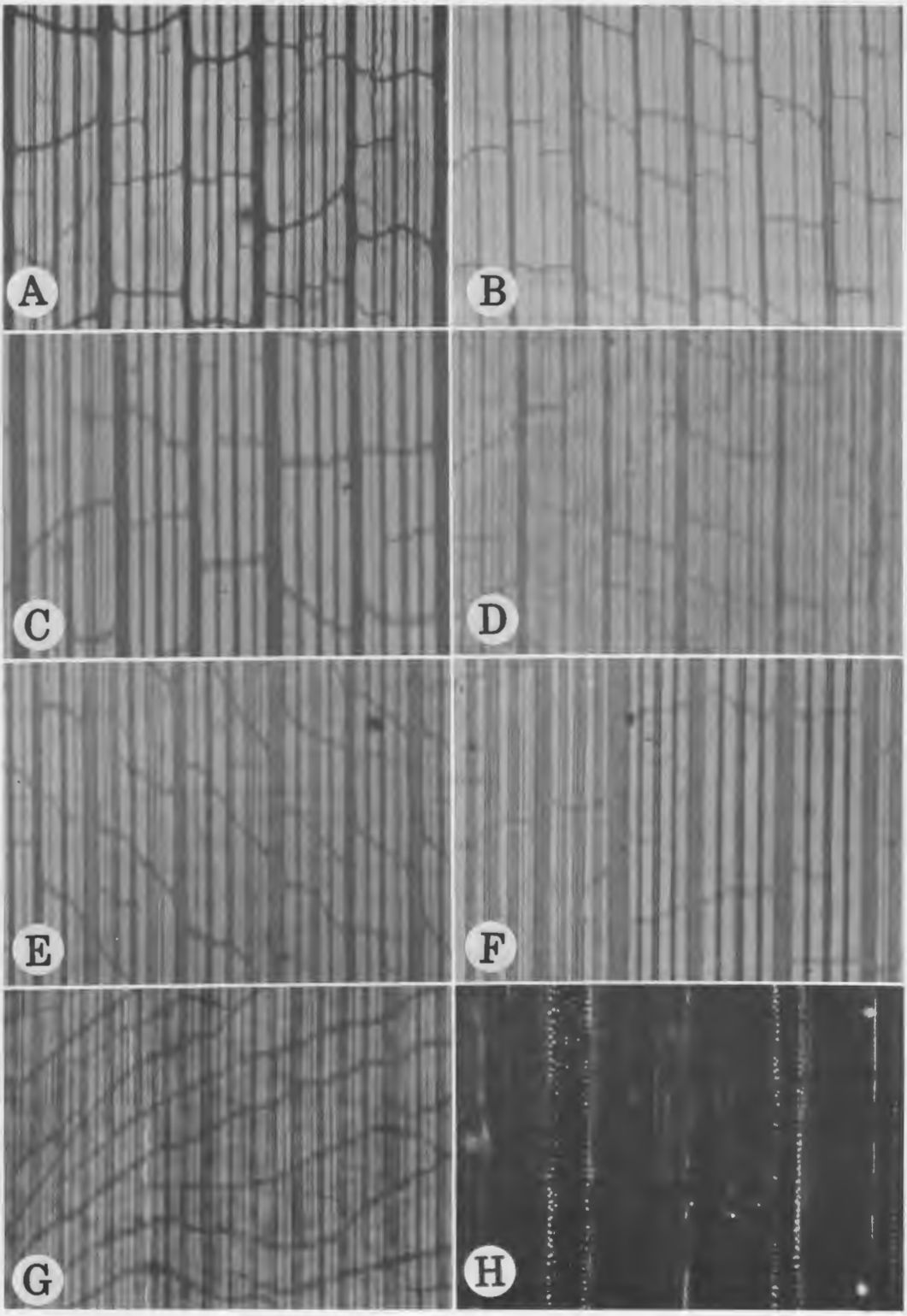
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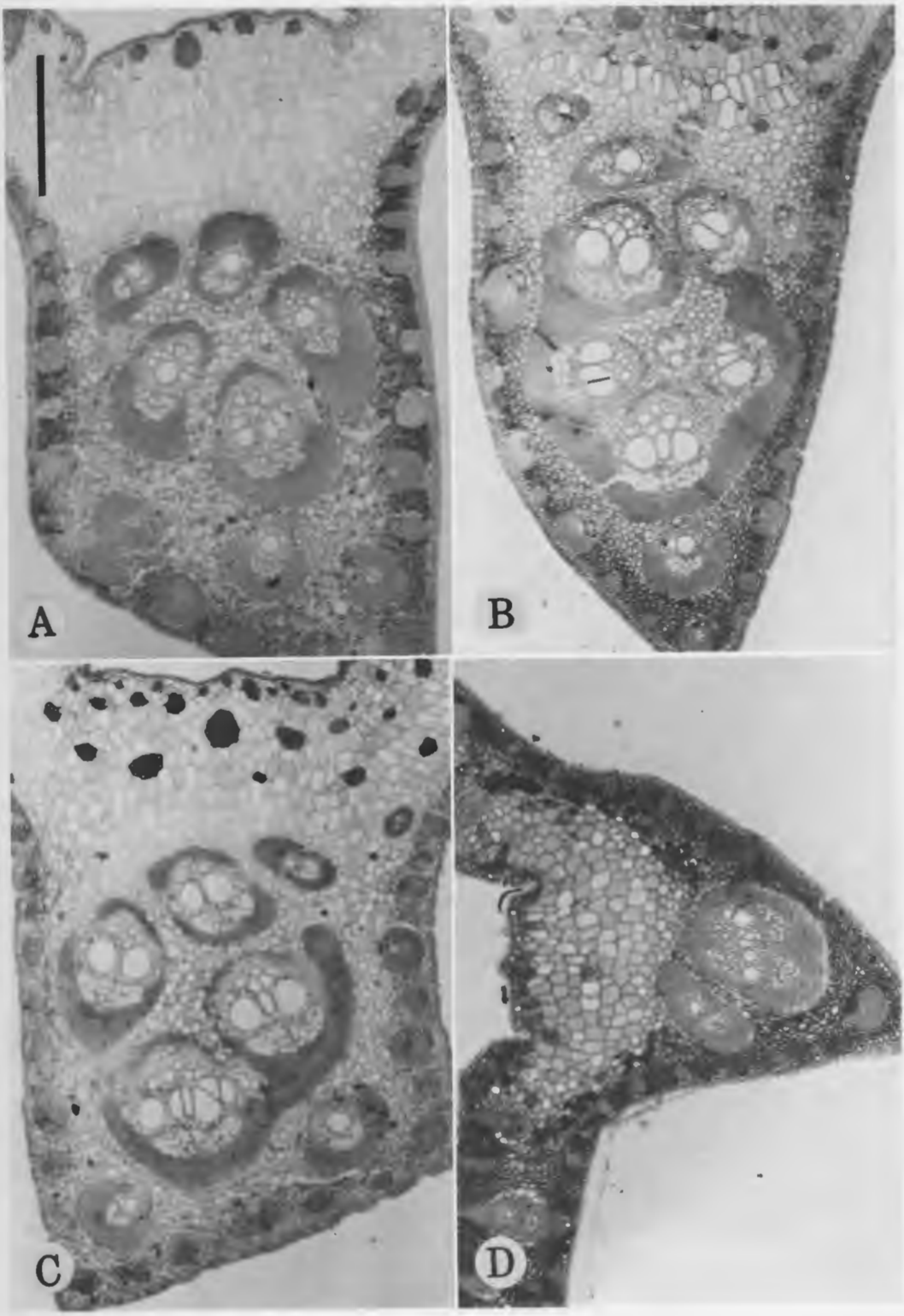
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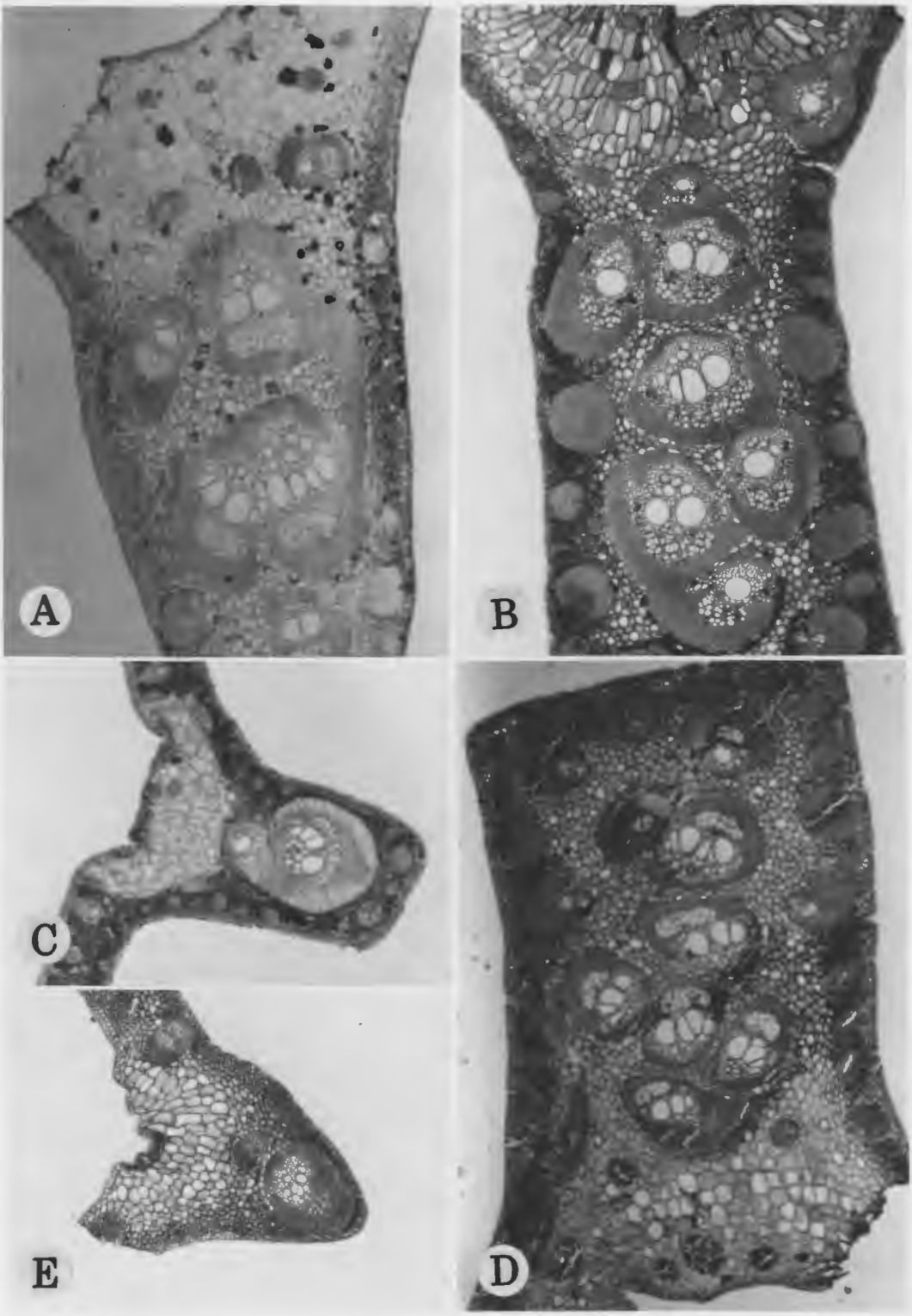
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specific level to resolve taxonomic questions. Exceptions are the studies by Balick and Cooper-Driver (*in* Balick 1986) on *Oenocarpus* and *Jessenia* (Arecoideae), Madulid (1980) on *Plectocomia* (Lepidocaryoideae), Williams, Harborne, and Glassman (1985) on *Attalea* and its allies (Arecoideae), and Zona and Scogin (1988) on *Washingtonia* (Coryphoideae). In all cases, differences and similarities in flavonoid profiles assisted in delimiting species or species groups; although, in the case of *Attalea,* a certain amount of infraspecific variation was detected.

Sabal has received only cursory examination by phytochemists (Harborne et al. 1974; Williams et al. 1973). An in-depth examination of flavonoid aglycones and C-glycosides was undertaken with the hope that variation in flavonoid constituents would shed light on certain taxonomic problems and phylogenetic relationships.

Materials and Methods

Leaf samples were obtained from wild and cultivated plants (Appendix 1); material from two taxa (*S. guatemalensis* and *S. miamiensis*) was not available. Samples were dried prior to flavonoid extraction and the analysis followed the methods outlined in Zona and Scogin (1988).

A presumptive test for negatively charged flavonoids was performed in the following way: flavonoids were extracted in 85% methanol for 1 h at room temperature, reduced in volume, and chromatographed in two dimensions in TBA and HOAc. Spots were visualized under ultraviolet light with and without ammonia vapor. Negatively charged flavonoids were recognized by their distinctive comet shaped spots and by their low Rf values in the TBA.

Saponins were presumed present if a stable foam persisted in an aqueous solution for more than 20 minutes. This test was performed on most species during aglycone preparation and extraction.

More than one individual was sampled for most of the species. In many instances intraspecific variation in the flavonoid profiles became apparent. In these cases it was assumed that the greater number of compounds were present but that some of the compounds were not present in detectable amounts.

The replacement of flavonols by flavones is thought to be a specialized characteristic within angiosperms (Bate-Smith 1962; Harborne 1966), as is O-methylation (as in tricin). Isoorientin and orientin are not thought to be interconvertible because C-glycosylation is an early biogenetic step, not merely a late or terminal C-glycosylation of luteolin (Wallace, Mabry, and Alston 1969). For this reason, orientin and isoorientin, although similar, are considered independent characters.

Results

The results are presented in Table 2. Only four aglycones and C-glycosides were detected from the leaves of *Sabal.* Tricin, a methylated flavone, is present in all samples of all 13 species. Orientin and isoorientin, both flavone C-glucosides,

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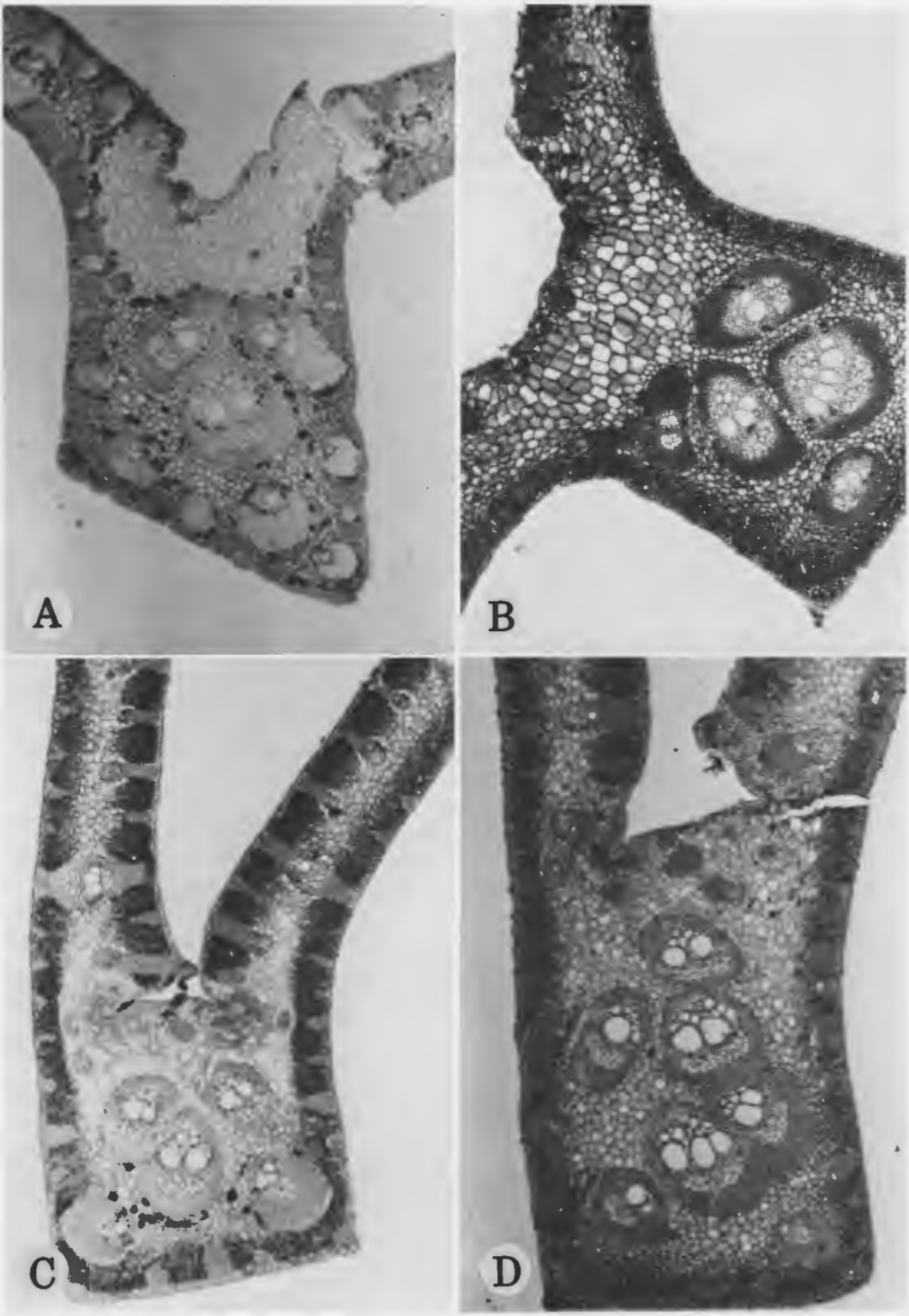
Fig. 11. Midvein transections of *Sabal.*—A. *S. guatemalensis* (*Moore 8209*).—B. *S. maritima* (*Zona et al. 298*).—C. *S. mauritiiformis* (*Zona et al. 141*).—D. *S. mexicana* (*Zona et al. 221*).—E. *S. minor* (*Perkins & Herring 987*). (Scale as in Fig. 10A.)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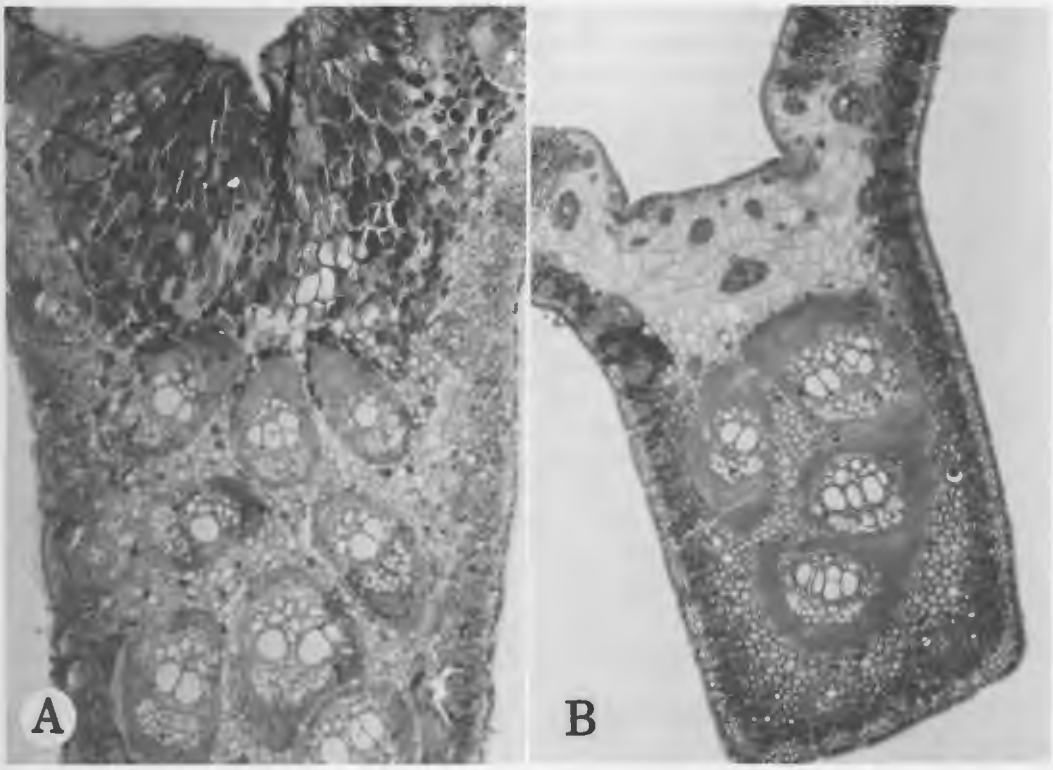

Fig. 13. Midvein transections of *Sabal.*—A. *S. uresana* (*Zona et al. 257*).—B. *S. yapa* (*Zona et al. 144*). (Scale as in Fig. 10A.)

were detected in 13 and 11 of the taxa, respectively. A fourth and apparently rare compound, vitexin, another flavone C-glycoside, was seen in two taxa. Procyanidin was detected, either strongly or in trace amounts, in about half the species. Saponins and negatively charged flavonoids were detected in 11 and 10 species, respectively.

Two-dimensional chromatography of methanol extracts (viz., glycosides) demonstrated the abundance of flavonoids in *Sabal.* The spots were too numerous to allow further analysis of the glycoside profile of each species.

Discussion

Eight species (*Sabal causiarum, S. etonia, S. maritima, S. mauritiiformis, S. mexicana, S. pumos, S. rosei,* and *S. yapa*) show intraspecific variation in detectable C-glycosides. *Sabal mauritiiformis* and *S. mexicana* are widely distributed species and one might suppose that these taxa might have diverged phytochemically at the extremes of their ranges. However, *S. etonia, S. pumos,* and *S. rosei*

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Fig. 12. Midvein transections of *Sabal.*—A. *S. miamiensis* (*Small & Nash s.n.*).—B. *S. palmetto* (*Zona 158*).—C. *S. pumos* (*Zona 250*).—D. *S. rosei* (*Zona 248*). (Scale as in Fig. 10A.)

Table 2. Foliar flavonoid aglycones, C-glycosides, and saponins of 13 of 15 species of *Sabal* and outgroups. Key: 1 = tricin; 2 = orientin; 3 = isoorientin; 4 = vitexin; 5 = procyanidin; 6 = saponins; 7 = negatively charged flavonoids. N = sample size, + = detected, − = not detected, T = trace, ( ) = not detected in all samples. Usually, only one sample per species was tested for the presence of saponins and negatively charged flavonoids.

		Flavonoids and saponins						
	N	1	2	3	4	5	6	7
Sabal bermudana	3	+	+	+	−	(T)	+	+
S. causiarum	4	+	+	(T)	−	(T)	(+)	+
S. domingensis	1	+	+	T	−	+	−	+
S. etonia	2	+	+	(+)	−	T	T	−
S. maritima	4	+	+	+	(T)	+	(+)	+
S. mauritiiformis	2	+	(+)	−	−	−	T	−
S. mexicana	2	+	(+)	(T)	−	−	+	+
S. minor	3	+	+	−	−	−	−	−
S. palmetto	5	+	+	+	−	(T)	(T)	+
S. pumos	3	+	+	(+)	−	T	T	+
S. rosei	4	+	+	(+)	−	+	T	+
S. uresana	2	+	+	+	+	T	T	+
S. yapa	3	+	(+)	(+)	−	−	T	+
Brahea dulcis	1	+	+	+	+	+	−	+
Washingtonia filifera	1	+	+	+	+	+	−	+

are narrow endemics (*S. causiarum, S. maritima,* and *S. yapa* less so), yet these appear to show as much intraspecific variation as the wide ranging species. These discrepancies may represent quantitative or qualitative intraspecific (i.e., interpopulational) differences, but the exact nature of the variation cannot be discerned at this level of inquiry.

Because of the significant amount of variation in the flavonoid profiles of many species, systematic conclusions based on flavonoid data are made only tentatively. Lack of variation in tricin and abundant unaccountable infraspecific variation in orientin and isoorientin all but excludes these data from the phylogenetic analysis. Vitexin (present in only 3 of 37 samples) seems to be rare in *Sabal,* but its rarity may reflect the difficulty in the reliable detection of compounds present in small quantities. A similar difficulty in applying variable flavonoid data to phylogenetic questions was encountered by Williams et al. (1985), who when faced with such variation were unable to draw systematic conclusions from their data. Saponins, procyanidin, and negatively charged flavonoids have been incorporated into the phylogenetic analysis.

A matter of particular interest, and one not apparent in Table 2, is the localization of procyanidin within the leaf tissues as confirmed by anatomical studies. Procyanidin was detected in *S. causiarum, S. domingensis, S. maritima* (all of the Greater Antilles), *S. rosei, S. pumos,* and *S. uresana* (all of western Mexico), as well as *S. bermudana* and *S. palmetto.* In the Antillean species, *S. palmetto,* and *S. bermudana,* procyanidin is localized in tannin sacs scattered through the mesophyll and surrounding the bundle sheath extension. In *Sabal rosei,* procyanidin is present in abundant tannin sacs within the mesophyll. *Sabal pumos,*

in which procyanidin is present in only trace amounts, has far fewer tannin sacs, compared with *S. rosei.* In contrast, *S. uresana* has a mesophyll essentially devoid of tannin sacs but has large amounts of tannin deposited in the bulliform cells (expansion cells) found along the midvein and suture vein (i.e., in the axil of each plication in the leaf). These tannin deposits can be shown to be procyanidin by extracting lamina tissue minus the veins, whole lamina tissue, and vein tissue. Only the latter two samples yield detectable levels of procyanidin.

Much has been written concerning the function of flavonoids in plants as herbivore deterrents (Levin 1971 and references therein). Certainly, if the major function of flavonoids is herbivore deterrence, *Sabal* palms are well protected. Flavonoids, in conjunction with anatomical/chemical protection mechanisms (viz., silica bodies, raphides, fiber), would then form a seemingly impenetrable protective phalanx around vital tissues.

Recent work in the area of phytochemical ecology suggests a correlation between the duration of leaves and the chemicals invested in their defense (Chabot and Hicks 1982; Cooley, Bryant, and Chapin 1985; Mooney and Gulmon 1982). Leaves of *Sabal* palms are evergreen and persist for more than one year (Zona pers. obs.). Large leaves of palms represent a considerable investment of photosynthates and are not rapidly replaced, even in areas of seemingly abundant resources. The prediction by Mooney and Gulmon (1982) that plants in resource-limited environments will defend their leaves rather than replace them seems justified in the case of *Sabal.*

Levin (1971), however, suggested that the most heavily defended plants are not just those with long-lasting leaves but rather those which are late successionary, tropical *K* strategists, i.e., those plants of predictable habitats. Plants of nonpredictable habitats (weeds, temperate plants, and early successionary *r* strategists) are less likely to invest heavily in defense. Apparentness to herbivores is implicit in Levin's argument. *Sabal* does not comfortably fit Levin's model. *Sabal* is typically a weed of tropical grasslands, wetlands, or pastures—all unpredictable habitats—and appears to have many characteristics of an *r* strategist (early succession or canopy gap colonizer, high annual rate of fruit set, small seeds). Unlike many herbaceous or perennial weeds, *Sabal* has large, long-lived leaves. Flavonoid data would seem to support the hypothesis that defense of leaves is more positively correlated with the longevity of the leaves (predictability in time) than with habitats (predictability in space).

REPRODUCTIVE BIOLOGY

Pollination

Despite its abundance and relative accessibility, *Sabal* has been largely ignored by biologists interested in the interactions between plants and their pollen vectors. To date there are only two published accounts of pollination in *Sabal* in its native habitat; *Sabal palmetto* was studied by Brown in several localities in the southeastern U.S. (Brown 1976), and *S. etonia* was studied by Zona (1987) in southern Florida. Knuth (1904) reported observations made on *Sabal* (spp. unknown) cultivated in Indonesia. Knuth (1909) cited work by Delpino who studied the pollination of *S. minor,* but apparently Delpino made his observations on palms

cultivated in Europe. What follows are observations by the author of pollinators and flower visitors along with a discussion of pollination ecology as it relates to the reproductive isolation of species of *Sabal.*

The pollination biology of *S. bermudana* is quite readily understood: the principal pollen vector is the introduced European honeybee, *Apis mellifera.* Prior to the widespread naturalization of the honeybee, *Megachile pruina pruina,* an *Augachlora* species, and a *Halictus* species may have had important roles in the pollination of this palm; however the latter two species have not been seen in this century and are thought to be extinct. The *Megachile* is thought still to exist in small numbers on Nonsuch I. but is absent from the main island.

The principal pollinator of *S. etonia* is a member of the Megachilidae, *Megachile albitarsus* (Zona 1987). Other solitary bees are important, viz., *Megachile xylocopoides, Augachloropsis metallica, Xylocopa micans,* and *Colletes mandibularis,* as is *Apis mellifera.* Flies of the families Syrphidae and Bombyliidae play a minor role in pollen transport. This species is slightly protandrous.

Brown (1976) reported the major pollinators of *S. palmetto* to be the halictid bees *Augachlora pura pura, Agapostemon splendens,* and *Dialictus* spp. The introduced honeybee is also an active pollinator. Brown (1976) stated that the species is protogynous.

Sabal mauritiiformis was observed in Panama, where its flowers are visited and likely pollinated by bees of the genera *Dialictus* and *Augachloropsis,* both of the Halictidae. In Trinidad, this species is visited by numerous bees.

Sabal palmetto and *S. maritima* growing in the Jardín Botánico Nacional de Cuba, Havana, are visited by numerous species and individuals of Hymenoptera, viz., bees and wasps. Flowers of *S. causiarum* were collected in the Dominican Republic also with numerous bees.

These observations suggest that Hymenoptera, especially solitary bees of the Megachilidae and Halictidae, are probably the principal pollinators for the genus. *Sabal* has many morphological traits that suit it to bee pollination. Several specializations for bee pollination, as listed by Henderson (1986), are apparent in all species of *Sabal*: a loose, open paniculate inflorescence exserted well beyond any sheathing or appressed bracts, sweet fragrance, and copious nectar production. To these criteria can be added hermaphroditic flowers that are short lived and that function during the daylight hours when bees are active and floral parts thin in texture.

The pattern of papillate cells found on the petals of *Sabal* may serve as nectar guides. The pattern may differentially reflect light and thus guide visitors to the septal nectaries. The petals of *Sabal* have not been examined under ultraviolet light to see if they show nectar guide patterns.

Sabal minor is reportedly protogynous (Knuth 1909) as is *S. palmetto* (Brown 1976), but *S. etonia* is weakly protandrous (Zona 1987). Morrow (1965) characterized the genus as "perhaps slightly protandrous." Further research is needed to resolve the contradictions in the literature.

Virtually nothing is known about whether hybridization in *Sabal* is possible and the relationship between hybridization and speciation in *Sabal.* Hybridization has been implicated (Zona 1985, 1987) in the origin of one species, but evidence is purely circumstantial. Mixed populations of two or three species can be found in the wild (Batabanó, Cuba, for example), but such populations appear to contain

no hybrid intermediates. Isolation barriers, beyond those of ecology, phenology, and pollinator specificity, are likely in play.

Seed Dispersal and Predation

The fruits of *Sabal* are typically black with a generous sweet pericarp surrounding 1–3 seeds. A few species, viz., the species of western Mexico, have large fruits which are often greenish brown rather than black and which have a very thick pericarp. *Sabal minor* has a small fruit with a notably thin, dry pericarp.

Hemsley (1885, p. 49) suggested that bird dispersal was the most likely explanation for the arrival of *Sabal bermudana* ["*S. blackburniana*"] to Bermuda, and drew a parallel between the dispersal and arrival of Bermuda's indigenous juniper (*Juniperus bermudiana* L.) and its indigenous palmetto. Guppy (1917, p. 16) noted that the Jamaican palmetto, *S. maritima* ["*S. umbraculifera*"] has fruits that are not buoyant and are seldom, if ever, found among beach drift. Guppy concluded that evidence weighed in favor of bird dispersal for *Sabal* and that the present distribution of the genus indicated past dispersal events.

In contrast, Brown (1973) suggested that water dispersal, hydrochory, was the principal mode of long-distance dispersal for *S. palmetto*. His experiments, floating mature dry fruit in 3.5% NaCl solution, showed that buoyancy varies among populations from low values of 0.0–3.0% floating after 3 weeks to 45.4% seeds afloat. Seed viability after 8 weeks in salt water ranged from 30% to 60%. Brown suggested that South Carolina and North Carolina coastal populations were derived from more southerly populations. He noted that northern populations had more buoyant fruits than southern populations, and suggested that this trend would be the expected outcome if northern populations were established by water-transported fruits from southern populations. Although Brown's hypothesis may be correct, Brown admits that confirmation awaits more rigorous testing. *Sabal mexicana*, another wide-ranging continental species, also has buoyant fruits (Zona pers. obs.).

Hydrochory may play a role in the dispersal of *S. minor*. This palmetto grows along stream banks and seasonally flooded areas where flooding corresponds with the fruiting season. Its pericarp is notably scanty. In a flotation experiment performed with 109 fresh *S. minor* fruits collected from Gainesville, Florida (*Perkins & Herring 987*), 43 seeds (39%) remained floating in distilled water after three days. After 7 days, only 6 seeds (6%) remained floating. Although post-flotation germination tests were not performed, the seeds appeared healthy and viable. These data would suggest that short term hydrochory is at least possible.

Animal dispersal (zoochory), a "syndrome" suggested by fleshy fruit (van der Pijl 1982), plays a role in the local dispersal of *Sabal* (Zona and Henderson 1989). Both birds and mammals are known to consume *Sabal* fruit. The birds *Mimus polyglottos, Turdus migratorius, Dendroica coronata, Corvus ossifragus,* and *Drycopus pileatus* are known to feed on fruits of *Sabal* (Martin, Zim, and Nelson 1951). Cruickshank (1950) reported the following birds feeding in *S. palmetto*: *Larus delawarensis, Quiscalus mexicanus, Aphelocoma coerulescens, Cardinalis cardinalis, Cyanocitta cristata,* and others. *Cyanocorax yncas* takes fruits of *S. mexicana* in Texas (Smith 1910), and *Crypturellus boucardi* feeds on fruits of *S. yapa* in Belize (Lancaster 1964). Fruits of *S. causiarum* are taken by

Columba leucocephala in Puerto Rico (Wiley and Wiley 1979), and *Aphelocoma coerulescens* takes fruits of *S. etonia* in Florida (Zona pers. obs.).

Mammals too play a large role in the dispersal of *Sabal* seeds in Florida; known dispersers are the Florida black bear, *Ursus americanus,* and the raccoon, *Procyon lotor* (Maehr and Brady 1984; Martin et al. 1951). Seeds of *S. palmetto* and *S. etonia,* in apparently viable condition, have been found in bear dung (Zona pers. obs.). The bat *Artibeus jamaicensis* is reported to feed on fruits of *S. palmetto* ["*S. parviflora*"] in Cuba (Silva 1979). Mammals, rather than birds, may play a greater role in the dispersal of the large-fruited *Sabal* of western Mexico, *S. rosei, S. pumos,* and *S. uresana.* Their fruits are more often greenish brown rather than black. Dull coloring and large size are suggestive of mammal dispersal (van der Pijl 1982).

The long-distance dispersal of *Sabal* by animals, notably birds, would agree with the biogeographical data, i.e., insular *Sabal* distributions. For example, the activities of the white crowned pigeon, *Columba leucocephala,* a nomadic frugivore found throughout the Antilles, Florida, and eastern Mexico, may contribute to the dispersal of *Sabal.*

Like many good colonists, *Sabal* is readily dispersed and probably does so by both hydrochory and zoochory. Dispersal is, and probably always has been, unpredictable and stochastic. The survival of most species of *Sabal* depends on exploiting new and disturbed environments, which are themselves unpredictable. *Sabal* has been remarkably successful in this regard.

In addition, the patchy distribution of *S. mauritiiformis* in Central and South America supports a long-distance dispersal explanation. This species skips over large areas of apparently suitable habitat in Honduras, Nicaragua, and El Salvador, only to reappear in extreme southeastern Costa Rica, eastern Panama and the Perlas Archipelago, north coastal South America and Trinidad. There is nothing in its present day distribution that suggests widespread extinction, rather its unpredictability suggests that the distribution is the result of chance dispersal events, most likely by birds. Not coincidentally, the most widely distributed species of *Sabal* (*S. causiarum, S. mauritiiformis, S. minor, S. palmetto, S. maritima, S. yapa*) are those with small fruits (less than 12 mm in diameter).

Species of *Sabal* are hosts to beetles of the genus *Caryobruchus* (Coleoptera: Bruchidae: Pachymerinae): adults feed on the nectar (Brown 1973) and larvae feed on the seed endosperm. The taxonomy of *Caryobruchus* is not settled, but clearly more than one species of the genus can be found throughout the range of *Sabal. Caryobruchus gleditsiae* is known from the southern United States (Brown 1973; Paxson 1969), the Gulf coast of Mexico (Olvera 1981), the Greater Antilles, and Bermuda (J. Kingsolver in litt.). A second, much larger species, tentatively referable to *C. curvipes,* is known from the larger fruited *Sabal* of western Mexico. It is not clear, however, if size of the adult bruchid is the direct result of a larger food source as a larva. Larvae of both species feed on *Sabal* in the wild but are known from seeds of cultivated coryphoid palms of other genera, e.g., *Pritchardia* Seem. & H. Wendl., *Serenoa* Hook. f., *Coccothrinax* Sarg., and *Phoenix* L. (Olvera 1981).

Adult *Caryobruchus* have been taken from the following species of *Sabal*: *S. bermudana, S. causiarum, S. domingensis, S. etonia, S. mauritiiformis, S. mexicana, S. minor, S. palmetto, S. maritima, S. pumos, S. rosei, S. uresana,* and *S. yapa.*

Brown (1973) discussed aspects of the life history of *C. gleditsiae* on *S. palmetto,* and found levels of predation as high as 92%. High levels (ca. 50%) are also known from *S. uresana* (Zona pers. obs.). Generation time is not known but is apparently short. *Caryobruchus* has the potential of being a highly efficient predispersal predator; however, Brown (1973) noted that level of predation can vary wildly from year to year (92% in one population in 1972, and 4% the following year). The causes for these fluctuations are not known.

In Florida, larvae of *C. gleditsiae* are parasitized by a wasp, *Heterospilus* sp. nov. (Hymenoptera: Braconidae). It has not been observed on other species of *Caryobruchus* and seems confined to Florida. Its life history is poorly known.

HISTORICAL BIOGEOGRAPHY

The modern distribution of *Sabal* is very different from its historical distribution. Fossil *Sabal* and *Sabalites* are known from the Soviet Union (Takhtajan 1958), Great Britain (Reid and Chandler 1933), Alaska (Wolfe 1972), Vancouver Island, and Japan (Kryshtofovich 1918), as well as New Jersey, Delaware, Maryland, South Carolina, Kentucky, Tennessee, Arkansas, Texas, Montana, Wyoming, Colorado, New Mexico, and California (Daghlian 1978; Noe 1936; Read and Hickey 1974). Given this distinctly north temperate distribution of fossils, how can we reconcile the presumed origin of the Arecaceae in West Gondwanaland (Moore and Uhl 1973) with the north temperate origin of *Sabal*?

Sabal is probably of Laurasian origin (Moore in Raven and Axelrod 1974). If palms arose in West Gondwanaland, then the progenitors of *Sabal* probably spread to Laurasia, where the genus evolved into recognizable form. The coryphoid palms of Laurasia (including *Sabal*) diversified independently from those taxa that remained in Gondwanaland (Dransfield 1987; Uhl and Dransfield 1987). Radiation in Laurasia followed by Neogene or Pleistocene extinction is a likely and parsimonious explanation for the modern and historical distribution of *Sabal.*

An alternate hypothesis, that *Sabal* evolved in West Gondwanaland and is recently beginning to invade North America (Corner 1966; Long 1974), completely ignores the fossil record that demonstrates: 1) that *Sabal* existed in North American long before a land connection was established between North and South America; and 2) that *Sabal* existed in Europe and Asia after the North Atlantic and Bering land bridges were severed. Furthermore, this hypothesis does not account for the absence of *Sabal* in some parts of Central America and in most of South America.

Sabal was a component of what Wolfe (1975) called the "boreotropical flora." The equable climate of the Tertiary (Buchardt 1978; Wolfe 1975) favored the rapid spread of a mixed flora with modern counterparts from temperate deciduous hardwood forest (e.g., *Juglans* L., *Carpinus* L., *Betula* L., *Liquidambar* L.) and tropical (especially paleotropical) rain forests (e.g., *Mastixia* Blume and members of the Icacinaceae). The classic London Clay flora, of which *Sabal* is an element (Reid and Chandler 1933), represents the boreotropical flora. There is no reason to suppose that the ecological requirements of *Sabal* in the Tertiary were any different than those of the genus today. In fact, *Sabal* is known from European fossil assemblages that contain many of the same genera that can today be found growing alongside *Sabal* in eastern North America, such as *Serenoa* Hook. f., *Leitneria* Chapm., and *Asimina* Adanson (Tiffney 1985).

A preponderance of evidence (Daghlian 1978; Dilcher 1971) suggests that the

paleoecology of *Sabal* was not appreciably different from its modern ecology: *Sabal* is likely to have grown in warm temperate to cool tropical regions with continually moist to seasonally dry moisture regimes, growing in broadleaf woodland, riparian, or perhaps even swamp communities.

Axelrod (1975) has suggested that *Sabal* was part of the Madro-Tethyan sclerophyllous flora. Borhidi (1985) recognized a Caribbean-Tethyan community to include many of the sclerophyllous vegetation types now found on Cuba. However, *Sabal* does not appear to possess the very characteristics that are used to define the sclerophyllous vegetation type: small, thick, hardened, heavily armed leaves. Furthermore, the extant members of the Madrean sclerophyllous flora, such as *Arctostaphylos* Adanson, *Cercocarpus* Kunth, *Mahonia* Nutt. (Axelrod 1975), do not occur with *Sabal*. *Sabal* is not known from Tethyan sclerophyll fossil floras, and Cornett (1986) has cast considerable doubt on the assignment of western North America fossil palms with unarmed petioles to *Sabal*.

Geologic History of North America

Several phenomena figure prominently in the geologic history of North America (including Mexico) since the origin of angiosperms in the Cretaceous: 1) land connection with Europe across the North Atlantic via the North Atlantic land bridge until approximately 49 MYBP (Eocene) and connection to eastern Asia via Beringia periodically throughout the Tertiary (Tiffney 1985); 2) isolation from South America until 5.7 MYBP (Upper Miocene) at which time the Panamanian isthmus arose; 3) massive orogeny in western North America; and 4) extensive glaciation during the Pleistocene.

Fragmentation of the range of *Sabal* began in the Eocene as the Rocky Mountains began to form (Early Eocene) and the North Atlantic land bridge was severed (Late Eocene) (Tiffney 1985). Orogeny of the Sierra Madre Occidental and Sierra Madre del Sur in the Miocene (Dressler 1954) further fragmented the range of *Sabal*, effectively isolating the western North American species from those in eastern North America. Western North American elements of the boreotropical flora retreated southward (Leopold and MacGinitie 1972), and uplift of the Sierra Madre Oriental in the Pliocene further isolated the species of western North America from those of the southern coastal plain. Residual populations of *Sabal* in the Central Plains, Great Basin, and Altiplana would have succumbed to the gradual climatic deterioration caused by inland rain shadows and cooler temperatures (Leopold and MacGinitie 1972).

Climatic deterioration in the Oligocene resulted in continual cooling of the Northern Hemisphere, eventually resulting in the glaciation of the Pleistocene (Tiffney 1985; Wolfe 1975). Such cooling and subsequent glaciation would have severely diminished the extensive distribution of *Sabal* in the Northern Hemisphere. As the populations of *Sabal* retreated southward in Eurasia, they were likely pinned against east–west running mountain ranges and eventually extirpated. In North America, *Sabal* was extirpated from the northern regions but was able to retreat to Mexico, the southeastern coastal plain, and the Antilles, as did *Nyssa* L., *Celtis* L., *Carya* Nutt., and many other genera (Dressler 1954; Graham 1973). The modern distribution of *Sabal* (with the possible exceptions of *S. mauritiiformis* and *S. palmetto*) is very similar to its distribution during the last glaciation.

Geologic History of the Antilles

The geologic history of the Antilles during the Cenozoic is exceedingly complex and has been the subject of much speculation (Hedges 1982; MacFadden 1980; Rosen 1975; Tarling 1980). The existence of the Caribbean Plate is now accepted, as is its eastward movement to its present position (Malfait and Dinkelman 1972). Post-Miocene marine transgressions, periodic uplift, and extensive subsidence, however, confound efforts to interpret geological data in a biologically meaningful way.

There is strong geologic evidence that the Greater Antilles arose *de novo* and that they were never attached to any continent (Malfait and Dinkelman 1972; Pregill 1981; Tarling 1980). The Greater Antilles arose in the late Cretaceous from subduction of oceanic lithosphere of the Caribbean Plate beneath ancestral southern Guatemala, Honduras, Nicaragua, the Nicaraguan Plateau, and the Cayman Ridge. The beginnings of Jamaica, Hispaniola, and eastern Cuba consequently arose as a volcanic arc parallel to the subduction zone (Pregill 1981). At the end of the Eocene, the Cayman Ridge broke away from the Nicaraguan Plateau and carried eastern Cuba, Jamaica, and much of Hispaniola to the northeast relative to North America. Subduction of the Atlantic oceanic crust beneath the Caribbean Plate resulted in volcanism that led to the formation of central Cuba, eastern Hispaniola, and Puerto Rico (Pregill 1981). Hispaniola, Jamaica, and Puerto Rico are moving eastward along the Puerto Rican Trench, although the rate of movement is in dispute (Hedges 1982).

Of greater interest to biogeographers are the dates at which the land masses became emergent. There is strong evidence that western and central Cuba have been emergent since at least the Eocene, although uplift of eastern Cuba did not take place until the late Miocene. The Virgin Islands, Puerto Rico, and part of Hispaniola may have been contiguous and emergent in the Oligocene (Graham and Jarzen 1969), although the evidence for this hypothesis is thin. Southern Hispaniola has been emergent since Pliocene times. Jamaica arose by seafloor uplift during the Miocene, but was largely inundated in the Oligocene (Buskirk 1985). As young as the Antillean land masses are, their coastal habitats (where *Sabal* is found) are even younger, since sea level changes during the Pleistocene ranged from about +20 m to −100 m or more (Mann, Taylor, Burke, and Kulstad 1984).

There is absolutely no geologic evidence for an Antillean–Guatemalan Land Bridge, as envisioned by Asprey and Robbins (1953) and more recently imagined by Borhidi (1985). The geologic interpretation presented by Malfait and Dinkelman (1972) does suggest that the Yucatán Peninsula has always been closest to Cuba, thus emphasizing the importance of the Yucatán-to-Cuba migration route. This migration route has had the greatest influence in the establishment of the Caribbean flora (Howard 1973; Raven and Axelrod 1974).

The Lesser Antilles arose quite independently from the Greater Antilles via volcanism in the late Eocene. The Lesser Antilles have not served as a northward migration route for *Sabal* (*Sabal* is not well-represented in South America), nor have they served as a southward migration route into South America. Their steep topography, with few coastal plains or swamps, may explain why *Sabal* has not become established in the Lesser Antilles.

Sabal certainly existed in North America prior to the uplift of the Antilles. As

Table 3. Characters and character states of *Sabal.*

Character	Plesiomorphic	Apomorphic
1. Aerial stem	present	absent
2. Clustered leaf segments	absent	present
3. Lamina texture	thick	thin or papery
4. Transverse commissures	short	long-looping
5. Transverse commissure position in mesophyll	middle	below the middle
6. Dorsal and ventral palisade height	equal	unequal
7. Bundle sheath extensions	present	absent or rare
8. Fiber bundles position in expansion region of midvein	axile	scattered or absent
9. Inflorescence posture	arcuate or cernuous	ascending
10. Orders of inflorescence branching	3	2 or 4
11. Dry petal condition	noncostate	costate
12. Fruit shape	longer than wide	spheroidal or oblate
13. Procyanidin	present	absent
14. Saponins	present	absent
15. Negatively charged flavonoids	present	absent
16. Tannins in midvein parenchyma	absent	present
17. Tannins around BSE and vascular bundles	absent	present
18. Tannins in hypodermis	absent	present
19. Tannins in bulliform cells of midvein	absent	present
20. Tannins peripheral to midvein expansion region	absent	present
21. Tannins within bundle sheaths	absent	present
22. Tannins around transverse commissures	absent	present

the Antilles were never joined to North America, the presence of *Sabal* on the Antilles can be explained only by over-water dispersal (long distance dispersal) in Eocene time or perhaps, for *S. palmetto* and *S. mauritiiformis,* even more recently.

PHYLOGENETIC ANALYSIS

The first, and until now, only phylogenetic hypothesis concerning the interrelationships of *Sabal* species came from Bailey (1944). Bailey's hypothesis was a short paragraph in his second treatment of the genus (Bailey 1944, p. 293). It is quoted here in its entirety:

> Although *Sabal minor* is the "oldest" species in terms of taxonomy and basis for the genus *Sabal,* one does not conclude that it is genetically primeval, or that it represents the main or dominant evolution in the group. Probably we should have had a more correct estimate of the genus if *S. palmetto* had happened to have been the descriptive starting point.

This statement, implying that *S. minor* is somewhat specialized and that *S. palmetto* is not, was the only clue Bailey gave to his concept of the evolution of the genus. His treatments (Bailey 1934, 1944), as well as those of Cook (1901) and Beccari (1907), are purely taxonomic in scope.

The taxonomic units used in this phylogenetic analysis are species of *Sabal* as

Table 4. Data matrix for cladistic analysis of *Sabal* and outgroups, *Brahea* (BRAH) and *Washingtonia* (WASH).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
BERM	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0
CAUS	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
DOMI	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1
ETON	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	1	0	1
GUAT	0	0	0	1	1	1	1	1	0	0	1	0	9	9	9	1	0	0	1	0	0	0
MARI	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0	0	1	0	0	0	1	1
MAUR	0	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0
MEXI	0	0	0	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
MIAM	1	0	0	0	0	0	0	0	0	0	0	1	9	9	9	1	0	1	0	1	0	1
MINO	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0
PALM	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	0
PUMO	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0
ROSE	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
URES	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0
YAPA	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0
BRAH	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WASH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

well as two outgroups, *Washingtonia filifera* (Linden) H. Wendl. and *Brahea dulcis* (Kunth) Mart. These species represent genera centered in Mexico that are thought to have had a geological and biogeographical history similar to that of *Sabal*; however, because *Sabal* is placed in its own subtribe (Uhl and Dransfield 1987), the outgroups are more closely related to each other than they are to *Sabal*. Phylogenetic hypotheses were tested using PAUP (version 2.4 by D. Swofford). The apomorphic and plesiomorphic conditions of the characters used in the analysis are presented in Table 3. The evolutionary direction for all characters was inferred by regarding the outgroup condition as ancestral. Polarization was also guided by the major trends in evolution outlined by Moore and Uhl (1982). The data matrix for 17 taxonomic groups and 22 synapomorphic characters is given in Table 4. The plesiomorphic condition was scored as "0," and the apomorphic condition was coded as "1." Missing data were scored as "9." The cladogram was constructed manually and checked against a consensus tree.

The cladogram is presented in Figure 14. It has 45 steps (character state changes) and several reversals and parallelisms. Figure 14 shows five major clades: the MINO, BERM, MARI, MEXI, and URES clades. The MINO clade consists solely of *S. minor*. Its lack of saponins isolates it from the remainder of the genus. *Sabal minor* has several apomorphies (1, 10, 15, and 18); however none is unique to this species. Its erect inflorescence position is autapomorphic.

The BERM clade consists of *S. bermudana, S. palmetto, S. etonia,* and *S. miamiensis*. It possesses synapomorphies for characters 18 and 21, both tannin location characters that are thought to have evolved several times on separate clades. The three continental species of this clade are joined by the presence of tannins peripheral to the expansion region of the midvein. This synapomorphy shows neither reversals nor parallelisms within the genus. Within the clade, *S. palmetto* is clearly isolated from *S. etonia* and *S. miamiensis*. *Sabal palmetto* is

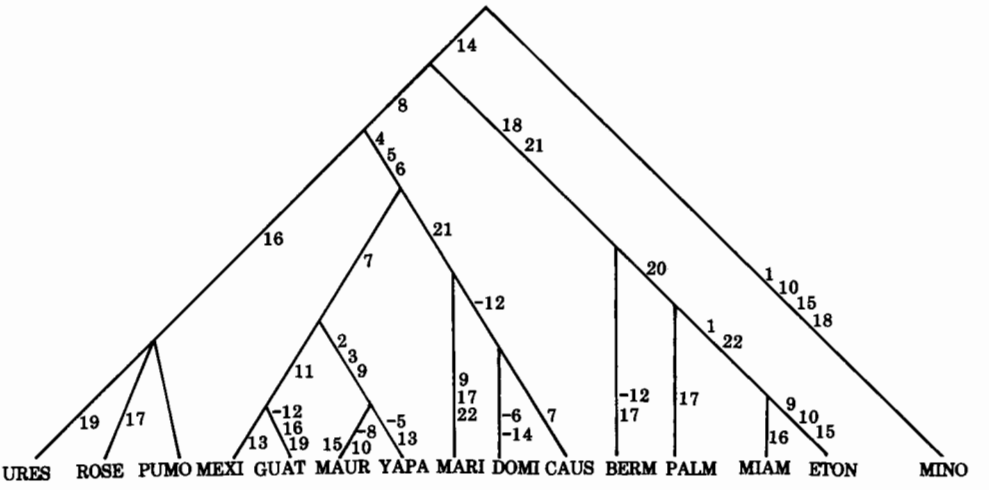

Fig. 14. Cladogram of proposed species relationships in *Sabal*. Branches are labeled with a four-letter code corresponding to the first four letters of each specific epithet. Numbers correspond to synapomorphies enumerated in Table 3. Negative numbers are character state losses.

relatively unspecialized and, as Bailey (1944, p. 293) noted, may well be similar morphologically to the ancestor of the genus. *Sabal etonia* lacks negatively charged flavonoids (15), but as material of *S. miamiensis* was unavailable, presence or absence of negatively charged flavonoids in *S. miamiensis* cannot be scored with certainty. The remaining clades (URES, MEXI, MARI) share the presence of scattered fiber bundles (or fiber bundles absent) in the expansion region of the midvein (synapomorphy for character 8).

The MEXI clade and the MARI clade form sister groups, defined by synapomorphies for characters 4, 5, and 6. Within the clades, there are reversals in both 5 and 6, but synapomorphy 4 (long-looping transverse commissures) is unaffected by parallelisms or reversals. The MARI clade is differentiated by the presence of tannins within the bundle sheath surrounding the vascular bundles (21). Within the clade, *S. domingensis* and *S. causiarum* are sister groups sharing a reversal to the ancestral condition, fruits longer than wide (12). The MEXI clade is defined by the loss of bundle sheath extensions (7). *Sabal mexicana* and *S. guatemalensis* share the derived condition petals costate when dry (11). This character appears nowhere else in the cladogram. *Sabal mauritiiformis* and *S. yapa* possess synapomorphies for leaf segmentation (clustered) and lamina texture (thin or papery), as well as inflorescence posture (ascending). Only the latter synapomorphy appears elsewhere in the cladogram. Each of these species has several morphological autapomorphies, not shown in Figure 14, that distinguish it from all other species of *Sabal*.

The final major clade is the URES clade comprising *S. uresana, S. rosei,* and *S. pumos*. These three species form an unresolved trichotomy and are united by the presence of tannins in the parenchyma of the midvein (16). *Sabal pumos* is the least specialized of the three and, in fact, is the least specialized in the entire genus. Of the characters considered here, the acquisitions of only three (8, 14, and 16) separate *S. pumos* from the hypothetical ancestral species.

The phylogenetic hypothesis proposed above is remarkable in its congruence with the biogeographic data, illustrated in Figure 15. The URES clade is clearly

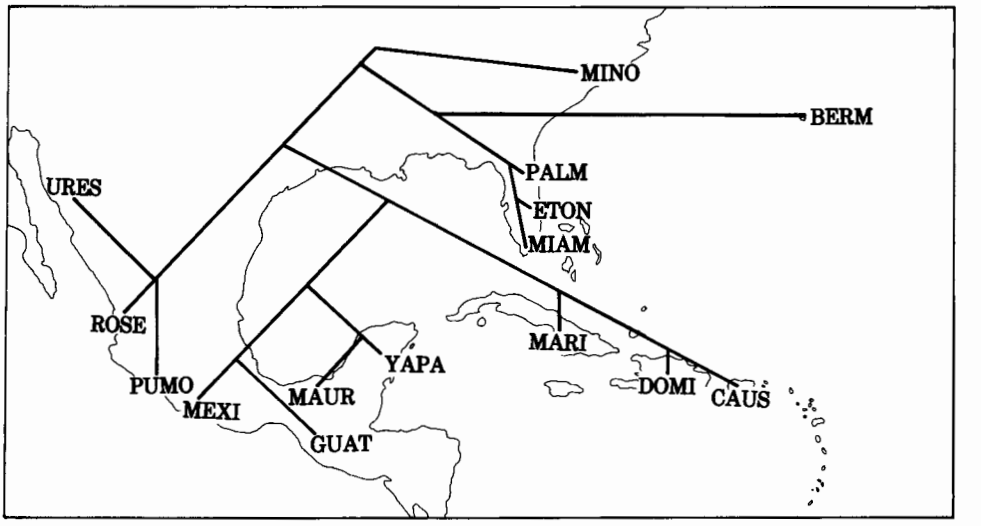

Fig. 15. Cladogram (as in Fig. 14) superimposed on a map of the Caribbean basin. Proposed phylogenetic relationships are highly congruent with biogeographical data.

isolated from the other Mexican species. The Antillean species share a common ancestor with the southern Mexican species and echo a well-documented floristic relationship between tropical Mexico and the Greater Antilles (Howard 1973).

Speciation in the genus has likely occurred by allopatric means. Allopatric speciation best explains the high correlation between the geographic distribution and the phylogenetic hypothesis. For example, orogeny of the Sierra Madre Occidental (and the Rocky Mountains to the north) may have isolated the common ancestor of the URES clade in western Mexico; subsequent ecological specialization could have led to further speciation in allopatry. In eastern Mexico, increasing aridity in the Tehuacán Valley or Isthmus of Tehuantepec may have fragmented the once continuous population of the ancestor of both *S. mexicana* and *S. guatemalensis.* Ecological allopatry may have been responsible for differentiation among *S. etonia, S. miamiensis,* and *S. palmetto.* Likewise, *S. yapa* and *S. mauritiiformis,* although geographically sympatric over portions of their ranges, are ecologically isolated—*S. yapa* inhabits slightly more arid habitats.

Since *Sabal* seeds are readily dispersed by birds and perhaps ocean currents, there is no need to believe that the Antillean species arose through vicariance events as have been proposed for other less vagile organisms (Buskirk 1985; McFadden 1980; Rosen 1975). *Sabal palmetto* (of Florida, Cuba, and the Bahamas) and *S. bermudana* (Bermuda) share a common ancestor but inhabit areas that were never contiguous, a fact which suggests that dispersal, rather than vicariance events, has played a greater role in the evolution of this clade and in the Antillean species. Historical events of dispersal, as an explanation for the origin of the Antillean species, are in agreement with the geological evidence and the known modes of dispersal in the genus.

TAXONOMIC HISTORY

The first mention in the literature of a palm referable to *Sabal* is that of P. Browne (1756), whose polynomial description of the Jamaican "Corypha (?) pal-

macea assurgens, foliis flabelliformibus semipinnatis, petiolis majoribus compressis" can be reliably ascribed to *Sabal* on the basis of the costapalmate ("flabelliformibus semipinnatis") leaves.

Species now assigned to *Sabal* entered the early botanical literature as *Corypha* L., *Chamaerops* L., and *Rhapis* L. f., genera now known to be native strictly to the Old World. Not surprisingly, eastern North American species first attracted the attention of post-Linnaean botanists, so *Corypha minor* Jacq., described in 1776, is the earliest binomial for a species now included in *Sabal.*

The genus *Sabal* was first proposed by Adanson (1763) in his "Familles des Plantes." The derivation of the name was not stated. Adanson clearly rejected the Linnaean system of binomial nomenclature when he described a genus/species of palm from the Carolinas (U.S.A.) with the uninomial *Sabal.* Parkinson (1987) has argued convincingly, at least in the case of *Sabal* and other genera first described as monotypic, that Adanson's use of unitary genus/species designations is in clear violation of International Code of Botanical Nomenclature Art. 20.4(b) which states that unitary designations of species are not to be regarded as generic names.

The genus name was validated by Guersent, who in 1804 published a description of *Sabal adansonii* and gave *Corypha minor* Jacq. as a synonym. As there were no alternate generic names proposed for *Sabal* between Adanson's description and its validation by Guersent, the genus name can correctly be attributed to Guersent.

Sabal appeared in various North American and Antillean floras (e.g., Chapman 1883; Grisebach 1864; Small 1903), and additional species were described or transferred to *Sabal* (Grisebach 1864; Hemsley 1885; Martius 1853; Nash 1896), but no comprehensive monograph existed. In 1901, O. F. Cook erected the genus *Inodes* to accommodate arborescent species of *Sabal* with strongly costapalmate leaves. The distinction between strongly costapalmate and weakly costapalmate was by no means clear, but this detail did not prevent Cook from describing five new species of *Inodes* and transferring to *Inodes* three more. In addition, between the inception of *Sabal* and its division by Cook, over 30 nomina nuda entered the botanical literature.

In 1907, the first monograph of the genus *Sabal* was published by O. Beccari. Beccari did not accept Cook's *Inodes,* transferred all of its species of *Sabal,* and described eight new taxa, bringing the total number of taxa of *Sabal* recognized to 18 species and one variety.

Subsequent to Beccari's monograph, several species were described as new (e.g., Beccari 1908, 1931; Small 1929) or transferred to *Sabal* (e.g., Burret 1933), until L. H. Bailey took up the genus for the first time in 1934. In that preliminary revision, Bailey (1934) recognized 22 species and one variety, two of the species being new. In 1944, Bailey published a second monograph of *Sabal* in which an unprecedented 26 species were recognized, six of which were new.

In H. E. Moore's (1963) checklist of palms and in a subsequent (Moore 1971*b*) addendum, he reduced a number of species to synonymy and recognized a total of 15 species. The current treatment includes three additional species long recognized by earlier botanists, synonymizes a few names, and replaces one name with an earlier, validly published name. A total of 15 species is recognized, and more than 45 nomina nuda are treated as such.

Cook's *Inodes,* despite its inherent artificiality, has not died quietly. Small (1933)

reduced *Inodes* to a subgenus within *Sabal.* This treatment was followed by subsequent students of the genus, including myself (Zona 1985), a disposition I am now pleased to correct.

TAXONOMY

SABAL Adanson ex Guersent, Bull. Sci. Soc. Philom. Paris 87:205–206. 1804.—Type: *Sabal adansonii* Guersent [=*Sabal minor* (Jacquin) Persoon].

Inodes O. F. Cook, Bull. Torrey Bot. Club 28:529. 1901. *Sabal* subgenus *Inodes* (Cook) J. K. Small, Man. s.e. fl. 239. 1933.—Type: *Inodes causiarum* O. F. Cook [=*Sabal causiarum* (Cook) Beccari].

Solitary, pleonanthic, hermaphroditic palms with aerial or subterranean woody unarmed trunks. Stem covered with leafbases or clean, obscurely to strongly ringed, becoming more or less smooth or striate and bare with age. Leaves few to numerous, alternate and spirally arranged, blade weakly to strongly costapalmate, glaucous or paler on the abaxial surface or not; petiole unarmed, convex abaxially, more or less concave adaxially, splitting at the base; hastula usually well developed on adaxial surface, obtuse to acuminate triangular, with peltate trichomes (these often caducous); hastula margin entire or undulate, erect, involute, or revolute; plication induplicate; leaf segments lanceolate, basally connate to connate for half their length or groups of two or three segments connate for almost their entire length, glabrous, glabrescent, or lepidote on abaxial surface of midveins, usually filiferous between leaf segments, apices acute or bifid and bearing a filament in each cleft; midveins prominent, transverse commissures obscure to conspicuous; stomata anomocytic, present on both surfaces or only the abaxial surface, plugged with cutin.

Inflorescence interfoliar, paniculate, erect, ascending, arcuate or cernuous, with 2–4 orders of branching; main axis bearing 2–5 sterile bracts above the prophyll; rachillae glabrous; flowers solitary, subsessile, subtended on the rachilla by a tanniniferous peduncular bract and bearing a single pedicillar bract, perfect, white, fragrant; calyx more or less cupulate with three tanniniferous lobes and composed of three connate sepals, carnose at the base, becoming membranous distally, margin hyaline; petals three, imbricate, elliptical, obovate, or spatulate, alternate with the outer whorl of stamens (basally connate in one species), margin hyaline and denticulate, membranous to chartaceous, spreading to reflexed at anthesis, basally adnate to the filaments; stamens six, outer whorl alternate with the petals, the inner whorl opposite the petals; filaments narrowly triangular to acuminate, basally connate; anthers hastate, dorsifixed, versatile, dehiscence latrorse by longitudinal slits; pollen yellow, ellipsoidal, monosulcate, exine reticulate; ovary of three carpels, connate, with a single stylar canal, superior, nectaries three, septal, style 0.5–1 mm long, stigma papillose, minutely three-lobed, dry; placentation basal-axile; ovules three, anatropous.

Fruit a 1–3-seeded berry, oblate, spheroidal, pyriform, or with 2–3 lobes when more than one seed develops; epicarp greenish-brown to black; mesocarp brown to black; endocarp brown, membranous, separating from the seed; seed oblate, flat to concave at the funicular end, brown; endosperm bony, homogeneous, white; embryo supraequatorial, equatorial or rarely subequatorial, minute.

Germination remote; eophyll simple, linear-lanceolate.

Chromosome number $n = 18$ (Bowden 1945; Eichhorn 1957; Read 1963, 1965, 1966; Sato 1946; Sharma and Sarkar 1956).

KEY TO THE SPECIES OF *SABAL*

1. Petals triangular-ovate, carnose, connate basally; calyx campanulate, not conspicuously costate when dry; Cuba and Yucatan Peninsula ..... 15. *S. yapa*
– Petals obovate to spatulate, membranous, alternate with and basally adnate to the filaments; calyx various but always costate when dry 2
2. Petals (even in bud) strongly costate when dry 3
– Petals not costate 4
3. Calyx cupulate; fruit spheroidal to oblate spheroidal, 14.8–19.3 mm in diameter; Texas, eastern and southern Mexico, and Yucatan Peninsula ..... 8. *S. mexicana*
– Calyx urceolate; fruit pyriform to oblate pyriform, 10.7–14.3 mm in diameter; southern Mexico and Guatemala ..... 5. *S. guatemalensis*
4. Inflorescence erect or ascending (especially early in development) 5
– Inflorescence arcuate or cernuous 8
5. Inflorescence with 2 (rarely 3) orders of branching 6
– Inflorescence with 3 or 4 orders of branching 7
6. Inflorescence ascending, bushy; fruit 9.0–15.4 mm in diameter; seed 6.4–9.9 mm in diameter; leaves strongly costapalmate, filiferous, hastula acute; Florida ..... 4. *S. etonia*
– Inflorescence erect, appearing sparse because internodes of main axis very long; fruit 6.4–9.7 mm in diameter; seed 4.4–6.9 mm in diameter; leaves weakly costapalmate, usually not filiferous, hastula obtuse; southeastern U.S.A. ..... 10. *S. minor*
7. Inflorescence with 4 orders of branching; leaf segments connate in groups of 2–3; lamina usually <0.1 mm thick; stomata present only on the abaxial surface; Mexico, Central America, South America, Trinidad ..... 7. *S. mauritiiformis*
– Inflorescence with 3 orders of branching; leaf segments connate regularly (not in groups); lamina 0.2–0.5 mm thick, stomata present on both sides; Jamaica and Cuba ... 6. *S. maritima*
8. Second order branches of inflorescence short, not exserted far beyond bracts of first order branches, thus rachillae appearing more or less fascicled; fruit strongly pyriform; Bermuda ..... 1. *S. bermudana*
– Second order branches of inflorescence well exserted beyond bracts of first order branches, thus rachillae not appearing fascicled; fruit various 9
9. Fruit greater than or equal to 15.5 mm in diameter, oblate or spheroidal 10
– Fruit less than 15.5 mm in diameter, pyriform, oblate-pyriform, or oblate 13
10. Inflorescence more or less cernuous, shorter than the petioles; tropical deciduous forests and oak forests, Rio Balsas Basin, Mexico ..... 12. *S. pumos*
– Inflorescence arching, equalling or exceeding the leaves in length 11
11. Stem subterranean; pinelands of South Florida ..... 9. *S. miamiensis*
– Stem aerial 12
12. Leaves evenly green; rachillae often thin and curling; western Mexico ..... 13. *S. rosei*
– Leaves glaucous; rachillae stiff; thorn forest, northwestern Mexico ..... 14. *S. uresana*
13. Transverse commissures of the lamina short and straight or obscure (when dry); southeastern U.S.A., Cuba, and Bahamas ..... 12. *S. palmetto*
– Transverse commissures of the lamina long-looping and conspicuous (when dry) 14
14. Fruit spheroidal (rarely oblate-pyriform), 7.1–10.8 mm in diameter, 7.5–10.4 mm high; seed 5.9–7.8 mm in diameter; British Virgin Islands, Puerto Rico and Hispaniola ... 2. *S. causiarum*
– Fruit pyriform, 11.5–14.1 mm in diameter, 11.0–14.4 mm high; seed 8.0–10.4 mm in diameter; Hispaniola ..... 3. *S. domingensis*

1. SABAL BERMUDANA Bailey, Gentes Herb. 3: 326. 1934.—Type: "Bermuda, Paget Marsh," 12 Jan 1922, *Bailey et al. 73* (lectotype, designated here: BH!).

Sabal princeps hort. ex. Beccari, Webbia 2: 59. 1907. *Sabal beccariana* Bailey, Gentes Herb. 4: 387. 1940.—Type: "from G. E. Mattei in Palermo [cultivated]," Jun 1907, *Mattei s.n.* (holotype: FI!).

Stout palm to ca. 7 m tall; trunk 20–35 cm DBH, gray, obscurely to prominently ringed with leaf scars. Leaves 15–25, evenly green, strongly costapalmate, filiferous; petiole 2.7–4.0 cm wide and 1–2 m long; hastula acute to acuminate, 8.5–18.5 cm long, glabrous or rapidly glabrescent, margin of hastula flat, involute or

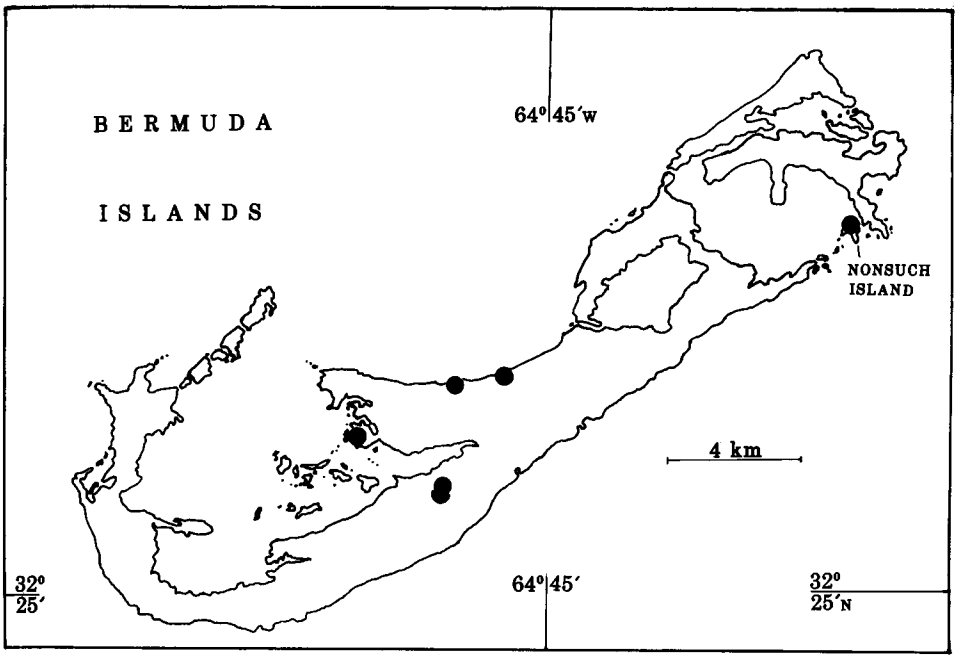

Fig. 16. Distribution of *Sabal bermudana*.

revolute, margin entire or undulate; segments 85–95 per leaf, connate for ca. 50% of their length, middle segment 90–140 cm long, 3.2–4.4 cm wide, 0.2–0.3 mm thick, transverse commissures prominent and short, apex bifurcate for 10–30 cm. Inflorescence arcuate with 3 orders of branching, not exceeding the petioles in length, sheathing bracts usually lepidote, penultimate branches short and often not emergent beyond the subtending bracts of the main axis, rachillae 4–8 per branchlet, 0.7–1.2 mm in diameter, 4–13 cm long, with (5–)6–7(–8) flowers per cm. Flower 4.0–6.0 mm long; calyx cupulate, strongly costate when dry, 1.7–2.5 mm long, 1.6–2.0 mm wide, sinuses 0.5–1.3 mm deep; petals obovate, noncostate when dry, membranous, 3.4–4.2 mm long, 1.3–1.9 mm wide; stamens spreading, filaments 3.1–4.5 mm long, adnate to the corolla for 0.7–1.5 mm, anthers ca. 1.3 mm long, 0.6 mm wide; gynoecium 2.2–3.9 mm long, ovary 0.6–1.0 mm high, 0.9–1.3 mm in diameter. Fruit pyriform, black, with a thick pericarp, 12.9–17.9 mm in diameter, 12.3–19.1 mm high; seed oblate-concave, 7.5–12.5 mm in diameter, 5.1–8.6 mm high, often with a sharp funicular beak; embryo supraequatorial, rarely equatorial. (Fig. 3D, 5A, 8A, 10A.)

Representative specimens.—BERMUDA. North shore, 14 Jun 1905, *Harshberger s.n.* (GH, MO, NY); Devonshire Parish, Palmetto Park, *Zona 289* (RSA); Hamilton Parish, Paynter's Vale, *Moore 3142* (F, GH, MICH); Paget Parish, Paget Marsh, *Brown & Britton 217* (A, GH, NY), *Ward 890* (BH); Pembroke Parish, *Collins 446* (GH, NY, P); Butterfield Nature Reserve, Point Shares, *Zona 284* (RSA); St. George's Parish, N end of Nonsuch Island, *Zona 283* (RSA).

Common names.—Bermuda palm, Bermuda palmetto.

Distribution and ecology (Fig. 16).—This species is endemic to Bermuda, growing in both dry upland and low marshy habitats. The type locality is Paget Marsh,

where it is found in association with *Acrostichum excelsum* Maxon, *Baccharis glomeruliflora* Pers., *Carex bermudiana* Hemsl., *Juniperus bermudana* L., *Myrica cerifera* L., and *Toxicodendron radicans* (L.) Kuntze (Hodge 1960). Introduced species, such as *Livistona chinensis* R. Br., *Nerium oleander* L., *Pimenta dioica* Merr., and *Pittosporum tobira* (Thunb.) Ait., have naturalized on the island and compete with native species, including *S. bermudiana.* Although not presently endangered, *S. bermudana* is highly vulnerable because of its island habitat.

Sabal bermudana flowers during June and July. The sweet fleshy fruit are produced in the fall and are consumed by birds including the introduced Kiskadee, *Pitangus sulphuratus.*

Discussion.—Watts and Hansen (1986) reported that *Sabal* pollen, presumed to be from *S. bermudana,* is a common element in sediment cores dating between ca. 10,000 and 9000 yr. B.P., a fact suggesting that *Sabal* has been part of the Bermuda flora for at least that long.

The taxonomic history of *S. bermudana* is also long. A provisional name, "*Sabal blackburnia*" was used by Glazebrook (1829), for a palm of unknown origin cultivated in England. Glazebrook (1829) illustrated globose fruits 19.2 mm in diameter and seeds bearing a beaklike funicular remnant. This latter characteristic is somewhat suggestive of the *Sabal* of Bermuda, but this epithet as used by Glazebrook must be rejected as a provisional name under Article 43.3 of the ICBN.

In 1830, the name *S. blackburniana* was validated with a brief description and reference to Glazebrook (1829) when it was included in Schultes and Schultes' Systema Vegetabilium. Although the provenance of the species was still unknown, the name was used by subsequent authors (e.g., Hemsley 1885) to refer to the *Sabal* of Bermuda. The protologue, however, includes a number of characteristics inconsistent with the Bermuda species: trunk with leaf scars, inflorescence shorter than the leaves, and fruit globose and 22.2 mm in diameter. The first two characteristics suggest *S. bermudana,* but the last two clearly do not. The fruits of *S. bermudana* are 12.9–17.9 mm in diameter and are strongly pyriform. Given the importance of fruit size and shape in recognizing species of *Sabal,* we cannot easily overlook this part of the description of *S. blackburniana.* Many specimens labeled *S. blackburniana* from European gardens represent *S. bermudana.* Nevertheless, in the absence of type specimens, the name *S. blackburniana* remains a nomen ambiguum and must be rejected.

The lectotype of *S. bermudana* was chosen from among the specimens seen by Bailey; it is one of the most complete specimens.

Sabal bermudana is unique in that age and growth rate of some individuals can be calculated with some degree of accuracy. The practice of tapping the stem of the palm just below the terminal bud for its sap (which was fermented to produce an alcoholic beverage, "bibby") has left visible scars. The practice was outlawed by the Governor of Bermuda in 1627 (Hodge 1960), yet trees with tapping scars are still common on the island. Trees so scarred are probably over 300 years old and yet appear to have grown only 3 m or so during that time, giving a growth rate of ca. 1 cm per year. Also visible in some palm stems are the bore holes of a species of woodpecker that is no longer found on the island (J. Madieros pers. com.).

2. SABAL CAUSIARUM (Cook) Beccari, Webbia 2:71. 1907. *Inodes causiarum* Cook, Bull. Torrey Bot. Club 28:531. 1901.—Type: "Porto Rico, Mayaguez to Joyuda," 14 Jun–22 Jul 1901, *Underwood & Griggs 154* (holotype: US!; isotype: NY!).

Inodes glauca Dammer in Urban, Symb. Ant. 4:127. 1903.—Type: "Porto Rico: prope Penuelas in valle fluvii ad Tallaboa poniente," Jul 1886, *Sintenis 4844* (holotype: B [destroyed], fragment: FI!; isotypes: GH! MO! P! US!).

Sabal haitensis Beccari, Ann. Roy. Bot. Gard. (Calcutta) 13:293. 1931 [pub. 1933].—Type: "Haiti," 1907, *Buch s.n.* (holotype: B [destroyed], fragment: FI!).

Sabal questeliana Bailey, Gentes Herb. 6:422. 1944.—Type: "St. Bartholomew [St. Barthelemy, Lesser Antilles, cultivated specimen]," 13 Jan 1939, *Questel 468* (holotype: BH!).

Massive palm to ca. 10 m tall; trunk 35–60 cm DBH, smooth and gray. Leaves 20–30, evenly green or glaucous, strongly costapalmate, filiferous; petiole 2.1–4.7 cm wide, 1–2 m long; hastula acute, 5.5–21 cm long, glabrous or glabrescent, margin revolute, flat, erect, or involute, entire or undulate, sometimes ridged abaxially; segments 60–120 per leaf, connate for ca. 40% of their length, middle segment 75–175 cm long, 2.6–5.8 cm wide, 0.2–0.4 mm thick, transverse commissures long looping and conspicuous, apex bifurcate for 20–43 cm. Inflorescence arcuate with 3 orders of branching, nearly exceeding the leaves in length, sheathing bracts usually glabrous or glabrescent, rachillae 11–20 per branchlet, 0.5–1.1 mm in diameter, 4.5–11 cm long, with (7–)8–9(–10) flowers per cm. Flower 3.7–5.2 mm long; calyx cupulate, strongly costate when dry, 1.3–2.0 mm long, 1.2–2.1 mm wide, sinuses 0.3–0.8 mm deep; petals obovate–long obovate, noncostate when dry, membranous, 3.0–4.0 mm long, 1.1–2.0 mm wide; stamens spreading, filaments 2.8–4.5 mm long, adnate to the corolla for 0.6–1.5 mm, anthers ca. 1.4 mm long and 0.7 mm wide; gynoecium 2.7–3.8 mm long, ovary 0.7–1.2 mm high, 0.8–1.1 mm in diameter. Fruit spherical or occasionally oblate-pyriform, black, 7.1–10.8 mm in diameter, 7.5–10.4 mm high; seed oblate concave, 5.9–7.8 mm in diameter, 4.3–5.7 mm high; embryo supraequatorial, rarely equatorial or subequatorial. (Fig. 3C, 5B, 8B, 9H, 10B.)

Representative specimens.—BRITISH VIRGIN ISLANDS. Anegada I., *D'Arcy 4950* (MO), *Britton & Fishlock 1061* (NY).—DOMINICAN REPUBLIC. Prov. AZUA: 18 km from Azua toward Baní, *Zona et al. 293* (RSA).—Prov. BARAHONA: near Barahona, *Fuertes 129* (GH, MO); 5.2 km W of Barahona-Azua highway on Barahona-Cabral road, near Laguna de Juan Santiago, *Gentry & Mejia 50684* (MO); 1 km S of Barahona at Playa Saladilla, *Zona et al. 290* (RSA); town of El Arroyo between Barahona and Enriquillo, *Zona et al. 291* (RSA); near Las Salinas and Cristobal between Cabral and Duverge, *Zona et al. 292* (RSA).—Prov. LA ALTAGRACIA: Bavaro, 27 km S of El Macao, *Zanoni et al. 36043* (JBSD).—HAITI. Dept. GRAND 'ANSE: Dame Marie, possibly originally cultivated, *Ekman 10507* (NY), 6 km S of Jérémie, near Marfranc, *Bartlett 17288a* (MICH).—Dept. SUD: Les Cayes, *Bailey 291* (photo only, BH), Habitation Tombeau, *Bailey 298* (BH).—PUERTO RICO. Without definite locality, *Britton et al. 1775* (NY); Guanajibo, near Mayaguez, *Bailey 18* (BH, MO); Isabela, 21 Apr 1921, *Barker s.n.* (BH); Joyuda, *Britton et al. 2403* (MO, NY), Peñuelas, *Bailey 43* (BH, MO); Pta. Borinquen, *Bailey 46* and *328* (BH), *Britton 9404 & Britton* (NY); San Sebastian, near Hoya Mala, *Liogier et al. 28728* (NY); Yabucoa, *Sintenis 5286* (FI, GH, MO, P); Yauco, near Mt. Duey, *Sintenis 3765* (GH).

Common names.—Palma de sombrero, palma de escoba, yaray (Puerto Rico), palma cana (Dominican Republic).

Distribution and ecology (Fig. 17).—*Sabal causiarum* is known from the western end of Puerto Rico and the island of Anegada in the British Virgin Islands as well

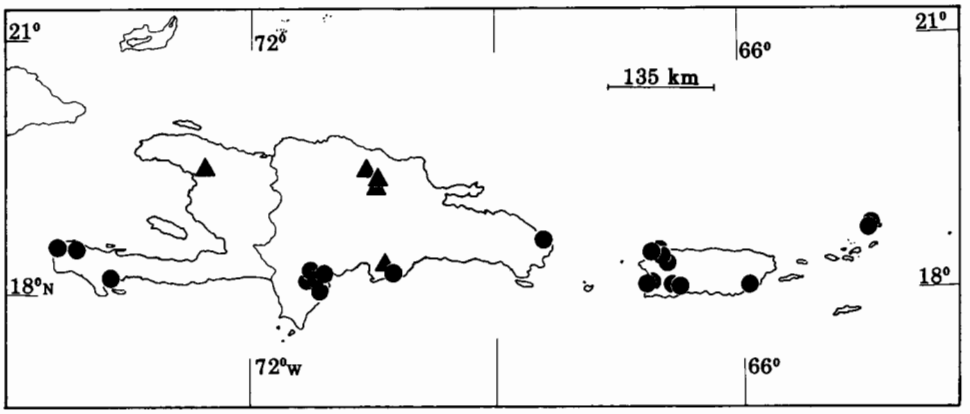

Fig. 17. Distributions of *Sabal causiarum* (circles) and *S. domingensis* (triangles) in Hispaniola, Puerto Rico, and the British Virgin Islands.

as Haiti and the Dominican Republic (Hispaniola). Its presence on the island of Hispaniola was first recognized by Moscoso (1943). It is reported by Questel (1941) to be naturalized on St. Barthelemy. It has been introduced on Guadeloupe, where it persists after cultivation.

In Puerto Rico, *Sabal causiarum* grows in the Subtropical Moist Forest Zone (Ewel and Whitmore 1973) in sandy soil (Cook 1901) from sea level to 100 m in elevation. Common associates are *Cedrela odorata* L., *Delonix regia* (Bojer) Raf., *Erythrina poeppigiana* (Walp.) O. F. Cook, *Ficus laevigata* Vahl, *Hymenaea courbaril* L., and *Tabebuia heterophylla* (DC) Britton.

Sabal causiarum flowers in the months of April through August. The species in not endangered.

Discussion.—Dammer and Urban (1903) recognized another entity from Puerto Rico but stopped short of giving it a name. The description was based on a specimen in the Berlin herbarium (*Sintenis 3765*) and was questionably assigned to *S. causiarum* by Beccari (1907), who remarked that without more material he was unable to decide with certainty if this was indeed another species. A duplicate specimen (at GH) consists of a portion of an old infructescence with only two orders of branching. Dammer and Urban gave the seed size as 8 mm × 6 mm (only slightly large for *S. causiarum*). Given the morphological plasticity of *Sabal* and the lack of other similar specimens, we must conclude that *Sintenis 3765* represents a depauperate or otherwise aberrant individual of *S. causiarum.*

3. SABAL DOMINGENSIS Beccari, Webbia 2:49. 1907.—Type: "Sto. Domingo a Gurabo, 200 m," 10 May 1887, *Eggers 1678* (holotype: P!, fragment at FI!; isotypes: B?, M, photograph: GH!).

Sabal neglecta Beccari, Webbia 2:40. 1907.—Type: "St. Domingo," 1827, *Jacquemont s.n.* (holotype: B [destroyed], fragment and photograph: FI!; isotype: P!).

Massive palm to ca. 10 m tall; trunk ca. 60 cm DBH, smooth and gray. Leaves 20–30(?), evenly green, strongly costapalmate, filiferous; petiole ca. 3.7 cm wide and 1 m long; hastula acute, ca. 15.5 cm long, glabrous, margin erect, entire; segments ca. 90 per leaf, connate for ca. 30% of their length, middle segment ca. 106 cm long, ca. 2.5 cm wide and 0.2 mm thick, transverse commissures long

and conspicuous, apex bifurcate for ca. 39 cm. Inflorescence arcuate with 3 orders of branching, equalling or slightly exceeding the leaves in length, sheathing bracts glabrous(?), rachillae 11–18 per branchlet, 1.0–1.2 mm in diameter, 7.5–12 cm long, with 10–11 flowers per cm. Flower (based on *Eggers 1678*) 4.5 mm long; calyx cupulate, strongly costate when dry, 1.7 mm long, 1.3 mm wide, sinuses 0.6 mm deep; petals obovate, noncostate when dry, membranous, 3.5 mm long, 1.3 mm wide; stamens spreading, filaments 3.8 mm long, adnate to the corolla for 1.1 mm, anthers 1.2 mm long and 0.8 mm wide; gynoecium 3.0 mm long, ovary 1.1 mm high, 1.1 mm in diameter. Fruit pyriform, black, 11.5–14.1 mm in diameter, 11.0–14.4 mm high; seed oblate concave, 8.0–10.4 mm in diameter, 5.1–7.1 mm high; embryo supraequatorial, rarely equatorial or subequatorial. (Fig. 5C, 8C, 10C.)

Representative specimens.—DOMINICAN REPUBLIC. Prov. ESPAILLAT: Moca, near Santiago, *Bailey 237* and *238* (BH).—Prov. LA VEGA: near La Vega, *Bailey 240* (BH).—Prov. PERAVIA: street tree in Baní, *Sanders et al. 1674* (BH).—Prov. SANTIAGO: Gurabo, *Bailey 236a* (BH).—HAITI. Dept. ARTIBONITE: near Les Poteaux, NE of Gonaives, *Bailey 145* (BH).

Common names.—Latanier, latanier-chapeau (Haiti), palma cana (Dominican Republic).

Distribution and ecology (Fig. 17).—*Sabal domingensis* is found on the interior of the island of Hispaniola at ca. 150–1000 m in elevation. It is a common component of secondary successional vegetation. Bisse (1981) reported that a Hispaniolan palm (*S. domingensis* or *S. causiarum*) is present on the southeastern coast of Cuba; however, I have seen no specimens of either *S. domingensis* or *S. causiarum* from Cuba.

The species apparently flowers during the summer, from March through August.

Discussion.—*Sabal domingensis* is poorly represented in herbaria and poorly known, probably because of the confusion between it and *S. causiarum.* The above floral description is based solely on one set of measurements from a fragment of the holotype at FI and therefore does not represent the entire range of variation.

When Beccari described *Sabal domingensis* he indicated that examples of the type specimen may be found at Berlin, Paris, Munich, etc., but explicitly designated no holotype. Although Glassman (1972*a*) designated the Berlin specimen as a lectotype, the holotype is the specimen at P, fragments of which are in Beccari's herbarium at FI and are annotated in Beccari's hand.

This species has long been confused with *S. causiarum,* a species found on Puerto Rico and the southern coast of the Dominican Republic. The species are readily distinguished on the basis of fruit size: 11.5–14.1 (12.7 ± 0.7) mm in diameter and 11.0–14.4 (13.1 ± 1.0) mm high for *S. domingensis* versus 7.1–10.8 (9.8 ± 0.5) mm in diameter and 7.5–10.4 (9.4 ± 0.7) mm high for *S. causiarum.* A similar size difference is found in the seeds.

4. SABAL ETONIA Swingle ex Nash, Bull. Torrey Bot. Club 23:99. 1896.—Type: "Florida, vicinity of Eustis, dry sandy soil, exclusively in 'scrub'," 16–30 Jun 1894, *Nash 999* (holotype: NY!; isotypes: BH! GH! MICH! MO! P! US!).

Sabal adansonii Guersent var.? *megacarpa* Chapman, Fl. south. U.S., 2nd ed. 651. 1883. *Sabal megacarpa* (Chapm.) Small, Fl. s.e. U.S. 223. 1903.—Type: "South Florida," without date, *Garber s.n.* (lectotype [vide Zona and Judd 1986]: MO!).

Small understory palm to 3 m tall; trunk usually subterranean but may emerge to ca. 2 m, 15–25 cm in diameter, leaves 4–7, yellow-green, strongly costapalmate, filiferous; petiole 1.1–1.8 cm wide, 0.3–0.5 m long; hastula acute, rarely acuminate, 1.6–3.3 cm long, glabrous (very rarely glabrescent), margin of the hastula flat and undulate or erect, revolute, involute, or entire; segments 25–50 per leaf, connate for ca. 15% of their length, middle segment 35–64 cm long, 1.3–3.1 cm wide, 0.2–0.3 mm thick, transverse commissures short and conspicuous or obscure, apex bifurcate for 9–29 cm. Inflorescence ascending (but may be prostrate in fruit), not exceeding the leaves in length, with 2 (rarely 3) orders or branching and appearing very densely branched or bushy, sheathing bracts lepidote or glabrescent, rachillae 11–25 per branchlet, 1.0–1.2 mm in diameter, 6–13 cm long, with (6–)7–8(–9) flowers per cm. Flower 4.9–6.1 mm long; calyx cupulate, strongly costate when dry, 1.5–2.0 mm long, 1.5–1.7 mm wide, sinuses 0.5–0.7 mm deep; petals obovate, noncostate when dry, membranous, 3.5–4.7 mm long, 1.8–2.4 mm wide; stamens spreading, filaments 3.9–4.5 mm long, adnate to the corolla for 0.9–1.2 mm, anthers ca. 1.6 mm long and 0.8 mm wide; gynoecium 3.1–3.8 mm long, ovary 0.6–0.9 mm high, 0.9–1.0 mm in diameter. Fruit oblate spheroidal, brownish black, with a thick pericarp, 9.0–15.4 mm in diameter, 8.5–13.1 mm high; seed oblate concave, 6.4–9.9 mm in diameter, 5.4–6.7 mm high, funicular remnant smooth; embryo supraequatorial or equatorial. (Fig. 3B, 5D, 8D, 10D.)

Representative specimens.—U.S.A. FLORIDA: Brevard Co., 4 mi S of Scottsmoor, *Shuey 1974* (USF).—Broward Co., Ft. Lauderdale, open country, *Bailey 473* (BH).—Clay Co., NE side of Kingsley Lake, *Ward 5490* (FLAS); Goldhead Branch State Park, *Skean 850* (FLAS).—Dade Co., Coconut Grove, Jan 1923, *Peattie s.n.* (F); Buena Vista, *Moldenke 580* (MO); North Miami Beach, Greynolds Park (West), along Scrub Oak Trail, *Zona 68* (FLAS).—DeSoto Co., E side of Cunningham Road ca. 2.5 mi N of Fla 70, *Shuey 1983* (USF).—Highlands Co., Archbold Biological Station, 8 mi S of Lake Placid, *Wunderlin et al. 6691* (USF); Josephine Creek Scrub, US 27, S of Kuhlman, *Lakela 24890* (GH, USF); 3 mi N of DeSoto City, *Wunderlin & Fantz 6017* (USF); W of Lake Jackson along US 27, *Judd & Judd 2846* (FLAS, RSA); SW end of Lake Jackson, *Judd et al. 2498* (RSA); between Avon Park and Sebring, 10 Jun 1928, *Cook s.n.* (BH); N of Avon Park, *Small 11572* (NY); vicinity of Avon Park, *McFarlin 5706* (MICH); S of Sebring, *Bailey 101* (BH).—Lake Co., vicinity of Eustis, *Nash 1164* (BH, MICH); 6 mi N of Altoona, 4 Aug 1977, *Daubenmire & Daubenmire s.n.* (USF).—Manatee Co., scrub E of N fork of Manatee River, *Shuey 1705* (RSA).—Marion Co., Ocala National Forest, SW of Salt Springs, *Utech 86-842* (CM); 1 mi W of Central Lookout Tower, *Ward & Ward 1936* (FLAS); along Fla 19 half way between Salt Springs and junction with Fla 40, *Judd 2774* (FLAS); 7 mi S of junction with Fla 316 along Fla 19, *Zona 14* (FLAS, RSA); S side of Fla 316, E of Oklawaha River, *Perkins & McKinney 997* (RSA); near Oklawaha River, *Bailey 479* (BH).—Okeechobee Co., near Okeechobee City, *Bailey et al. 6212* (BH).—Osceola Co., scrub E of Alligator Lake, 27 Oct 1974, *Shuey s.n.* (USF).—Palm Beach Co., Jupiter, 19 Jul 1929, *O'Neil s.n.* (FLAS, US); Boynton Beach, E of Seacrest Blvd., NE of St. Joseph's Church and School, *Zona 116* (RSA) and *133* (RSA); Boca Raton, N side of Clint Moore Rd., W of I-95, *Zona et al. 63* (FLAS).—Polk Co., W of Frostproof along US 98, *Lakela 24809* (FLAS, GH, USF); S of Frostproof along US 27, *Judd 2840* (FLAS); between Lake Wales and Avon Park, *Godfrey et al. 63337* (FSU).—Putnam Co., N of Florahome, 16 May 1959, *Wilson s.n.* (FLAS).—St. Lucie Co., E of US 1, 0.5 mi N of Taylor Creek Bridge, *Ward 4922* (FLAS, FSU).—Seminole Co., N side of Fla 46, W of Geneva, *Shuey 1975* (FLAS).—Volusia Co., James Ormond County Park, *Zona 31* and *34* (FLAS).

Common name.—Scrub palmetto.

Distribution and ecology (Fig. 18).—*Sabal etonia* is endemic to the deep sand ridges of central and southeastern Florida. It is a common understory component of a sand pine/xerophytic oak community dominated by *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., *Quercus geminata* Small, *Q. myrtifolia* Willd., *Q.*

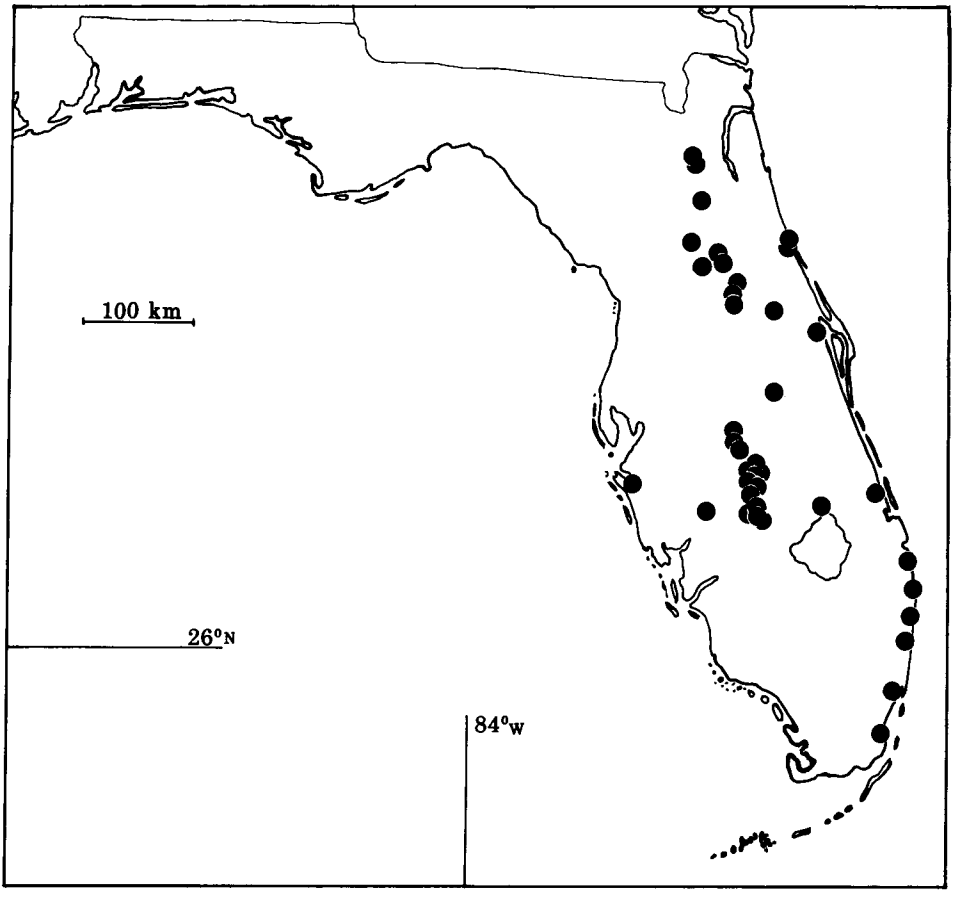

Fig. 18. Distribution of *Sabal etonia* in Florida.

inopina Ashe, and *Q. chapmanii* Sarg. (Harper 1914, 1915, 1927; Kurz 1942). Its ecology and distribution have been discussed more fully elsewhere (Mulvania 1931; Zona and Judd 1986).

Sabal etonia flowers from late May through July.

This species is not presently endangered; however, most of its habitat on the Atlantic Coastal Ridge in southeastern Florida has been destroyed by urban growth. In central Florida, its habitat has been largely cleared for agriculture. Large populations of *S. etonia* remain protected in the Ocala National Forest in the north and Archbold Biological Station to the south.

Discussion.—*Sabal etonia* is one of the few species in the genus that is not "weedy" but rather is characteristic of an undisturbed vegetation community, the sand pine scrub, a community rich in endemic plants and animals.

Its generally subterranean stem, ascending and bushy inflorescence (with generally only two orders of branching), and medium large fruits and seeds, along with its distinctive ecology, combine to make *S. etonia* readily distinguishable from all species in the genus.

5. SABAL GUATEMALENSIS Beccari, Webbia 2:68. 1907.—Type: "Guatemala," without date, *Skinner s.n.* (holotype: B [destroyed], fragment and photograph: FI!).

Robust palm to ca. 15 m tall; trunk 25–35 cm DBH, gray, with or without leafbases. Leaves 10–25?, evenly green, strongly costapalmate, filiferous; petioles 3.0–3.6 cm wide, ca. 1–2 m long, hastula acute, 14–18 cm long, glabrous or glabrescent, margin of hastula erect and undulate, occasionally entire; segments 80–100 per leaf, connate for ca. 30% of their length, middle segment 130–175 cm long, 2.8–5.7 cm wide, 0.2–0.4 mm thick, transverse commissures abundant, long and conspicuous (very rarely inconspicuous), apex bifurcate for 40–70 cm. Inflorescence arcuate with 3 orders of branching, equalling the leaves in length, sheathing bracts lepidote or glabrescent, rachillae 11–22 per branch, 1.0–1.4 mm in diameter, 5.5–14.5 cm long, with (8–)9–10(–11) flowers per cm. Flower 4.1–4.9 mm long; calyx urceolate, strongly costate when dry, 1.6–2.3 mm long, 1.0–2.1 mm wide, sinuses 0.4–0.9 mm deep; petals obovate-spatulate, costate when dry (apparent even in mature buds), membranous, 3.2–4.0 mm long, 1.2–1.9 mm wide; stamens ascending-spreading, filaments 2.8–4.4 mm long, adnate to the corolla for 1.2–1.8 mm, anthers ca. 1.3 mm long and 0.7 mm wide; gynoecium 3.0–3.9 mm long, ovary 0.6–1.5 mm high, 0.9–1.2 mm in diameter. Fruit pyriform to oblate-pyriform, black, 10.7–14.3 mm in diameter, 10.2–13.9 mm high; seed oblate concave, 7.7–11.2 mm in diameter, 4.9–7.2 mm high, with a beaklike funicular remnant; embryo supraequatorial, rarely equatorial. (Fig. 5E, 8E, 11A.)

Representative specimens.—GUATEMALA. Without locality, Aug 1887, *Conte di Solms s.n.* (FI).—Dept. FLORES: San Andrés, *Cook & Martin 186* (BH).—Dept. ZACAPA: Gualan, *Kellerman 5007* (BH), Carbañas, *Clausen 6213* (BH).—Dept. EL PROGRESO: *Moore 8209* (BH).—MEXICO. CHIAPAS: Mpio. Cd. Hidalgo, near R. Suchiate, *Bailey 577* (BH); Mpio. Carranza, slope at Soyatitan, *Laughlin 953* (BH).—OAXACA: Mpio. Chahuites, 10 km E of Chahuites toward Arriaga, *Pennington & Sarukhán 9512* (A, NY); Mpio. Tututepec, 4–5 km W of San José Progreso, *Zona et al. 180, 181* and *182* (RSA).—YUCATÁN: Mpio. Halacho, Halacho, *Quero R. 2328* (MO).

Distribution and ecology (Fig. 19).—*Sabal guatemalensis* is known from southern Mexico and adjacent Guatemala.

Collections of flowering material are known from December through May.

Discussion.—This species is poorly known and has long been regarded as conspecific with *S. mexicana,* with which it occurs in southern Mexico. Clearly the two are closely related, since they share certain morphological and anatomical features, such as petals strongly costate, long looping transverse commissures and absence of fully developed bundle sheath extensions. The two can be distinguished by characteristics of the calyx, fruit, and seed. The calyx is urceolate in *S. guatemalensis* (vs. cupulate in *S. mexicana*). Fruits are pyriform to oblate-pyriform, 10.7–14.3 (12.7 ± 0.9) mm in diameter and 10.2–13.9 (12.5 ± 0.9) mm high in *S. guatemalensis,* but they are spherical to oblate-spheroidal, 14.8–19.3 (17.2 ± 1.1) mm in diameter and 13.8–17.0 (15.3 ± 0.9) mm high in *S. mexicana.* The seeds of *S. guatemalensis* are smaller than those of *S. mexicana.*

6. SABAL MARITIMA (Kunth) Burret, Repert. Spec. Nov. Regni Veg. 32:101. 1933. *Corypha maritima* Kunth in Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp. 1:298. 1815 [publ. 1816]. *Copernicia maritima* (Kunth) Martius, Hist. nat. palm. 3:319. 1853.—Type: "littore australi Insulae Cubae prope pagum Bata-

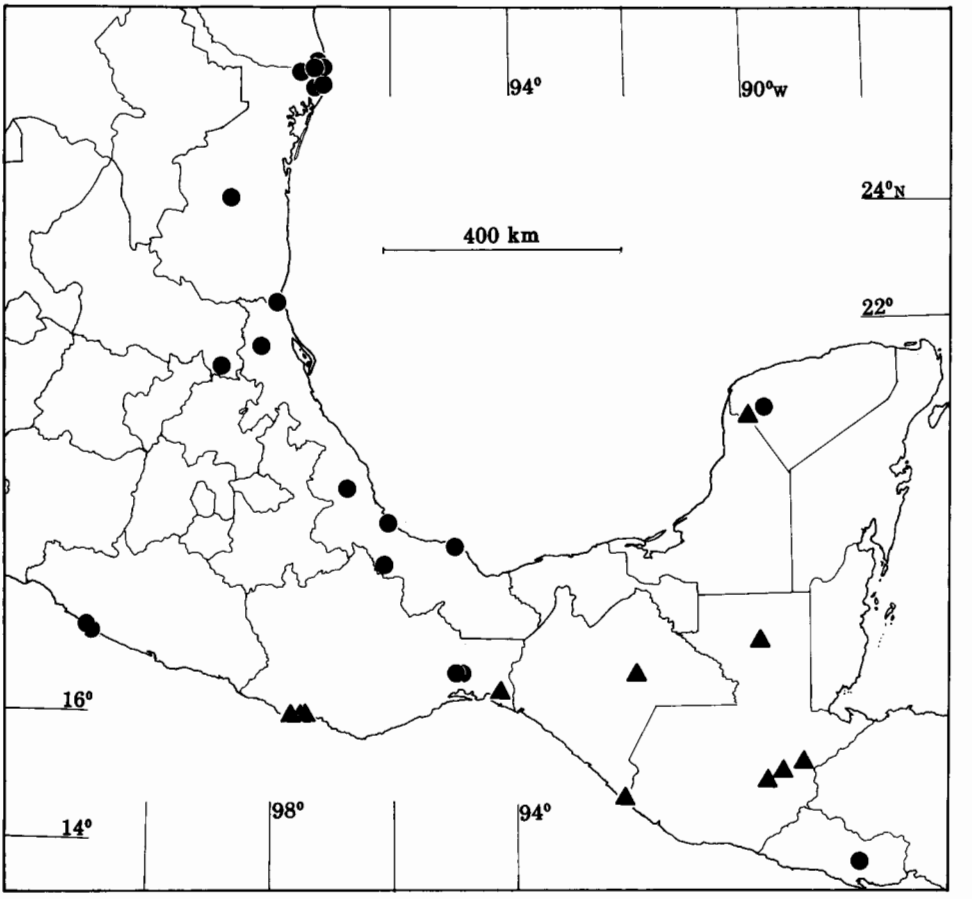

Fig. 19. Distributions of *Sabal guatemalensis* (triangles) and *S. mexicana* (circles).

bano," Mar 1801, *Bonpland 1355* (holotype: P-Bonpl.!, Field Museum neg. 38704, photograph: RSA!).

Sabal florida Beccari, Webbia 2:46. 1907.—Type: "Cuba, Santa Clara, district Cienfuegos," 7 May 1895, *Combs 292* (holotype: B [destroyed], fragment and photograph: FI!; isotypes: GH! NY! P!).

Sabal jamaicensis Beccari, Repert. Spec. Nov. Regni Veg. 6:94. 1908.—Type: "Jamaica, Pedro Bluff," 7 Sep [or 9 Jul?] 1907, *Harris 9736* (holotype: B [destroyed], fragment and photograph: FI!; isotypes: NY! P! US!).

Robust palm to ca. 15 m tall; trunk 25–40 cm DBH, gray, with or without persistent leafbases. Leaves 15–25, evenly green, strongly costapalmate, filiferous; petioles 3.3–5.0 cm wide, ca. 1–2 m long, hastula acute to acuminate, 10.0–24.0 cm long, usually densely lepidote, margin of hastula flat, erect, undulate, or entire, rarely involute or revolute; segments 72–110 per leaf, connate for ca. 35% of their length, middle segment 70–145 cm long, 2.4–5.3 cm wide, 0.3–0.5 mm thick, transverse commissures abundant and conspicuous, apex bifurcate for 10–70 cm. Inflorescence ascending with 3 orders of branching, equalling the leaves in length, sheathing bracts densely lepidote, rachillae 8–20 per branch, 0.9–1.3 mm in diameter, 6–15 cm long, with (7–)10(–13) flowers per cm. Flower 3.3–5.0 mm long;

calyx cupulate-urceolate, strongly costate when dry, 1.5–2.2 mm long, 1.7–2.2 mm wide, sinuses 0.4–1.1 mm deep; petals obovate, noncostate when dry, membranous, 2.8–4.3 mm long, 1.3–1.9 mm wide; stamens ascending-spreading, filaments 2.1–4.3 mm long, adnate to the corolla for 0.4–1.7 mm, anthers ca. 1.2 mm long and ca. 0.7 mm wide; gynoecium 1.9–3.4 mm long, ovary 0.4–1.1 mm high, 0.8–1.2 mm in diameter. Fruit oblate-pyriform to oblate-spherical, black with a thick pericarp, 8.5–14.2 mm in diameter, 8.4–12.6 mm high; seed oblate concave, 6.5–9.7 mm in diameter, 4.5–6.2 mm high, with a smooth (rarely somewhat beaked) funicular remnant; embryo supraequatorial, rarely equatorial. (Fig. 4B, 6A, 8F, 11B, 21A, B.)

Representative specimens.—CUBA. Between GRANMA and HOLGUIN (Oriente): Mir, sabana de la Cañada del Yarey, *León 15536* (GH).—LA HABANA: La Habana, cultivated in Jardín Botánico Nacional, transplanted from Candelaria, Pinar del Rio, *Zona 279* (RSA); Mpio. Alquizar, Sabana de Guanimar, swamps, *León 14178* (BH, GH); Mpio. Batabanó, wooded swamps, *León 13428* (GH), *León 14184* (BH, GH), *León 14576* (GH), *Bailey 12549* (BH).—LAS TUNAS (Oriente): Mpio. Las Tunas, Gamboa, *Bailey 15158* (BH).—JAMAICA. Cornwall Co.: Hanover Parish, Rutland Pen near Negril, *Read 1618* (BH); St. Elizabeth Parish, 0.8 mi N of Mountainside, *Proctor 38047* (IJ, MO, NY); Great Pedro Bay, *Britton 1252* (NY); Santa Cruz Mountains, Bideford District, SW of Malvern, *Webster & Proctor 5314* (A, IJ, MICH); Santa Cruz, W side of town, *Zona et al. 300* (RSA); between Mountainside and Black River, *Zona et al. 301* (FLAS, IJ, RSA); Westmorland Parish, near Little London, *Proctor 11110* (IJ); W edge of Little London, *Zona et al. 302* (FLAS, IJ, RSA).—Middlesex Co.: Manchester Parish, Little Mountain District, S side of Victoria Town, *Zona et al. 299* (FLAS, IJ, RSA).—Surrey Co.: St. Andrew Parish, Mona Hill, vicinity of Kingston, *Britton 371* (GH, MO, NY); upper N end of Dallas Mountain, *Patrick 193* (GH, IJ); Halls Delight, between Papine and Dallas, *Zona et al. 298* (RSA).

Common names.—Guana cana, guano blanco, guano rabo de cote, palma, palma cana, palmetto (Cuba), bull thatch (Jamaica).

Distribution and ecology (Fig. 20).—*Sabal maritima* is found in southern and western Jamaica and throughout Cuba, where it is found on sandy or limestone-derived soils from sea level to ca. 600 m. In Jamaica, its distribution corresponds closely to the distribution of very young soils. It is locally common in scrubby or disturbed vegetation and commonly persists in pastures in western Jamaica. In Cuba, it is usually found on poorly drained sands and clays of Quaternary age.

This species blossoms from March through September.

Discussion.—*Corypha maritima* Kunth is one of the oldest basionyms for a species now included in the genus *Sabal.* The type is sterile, and hence, the epithet has been treated as a possible synonym of *Sabal yapa* by Beccari (1912), a doubtful species by Bailey (1944), and, in violation of the ICBN rule of priority, as a synonym of *S. parviflora* (=*S. palmetto*) by Muñiz and Borhidi (1982). Thanks to P. Morat of the Laboratoire de Phanerogamie, Paris, the type was located and a fragment provided for anatomical study. Once its identity was established by anatomical study, the epithet was again available for use.

On Cuba, *S. maritima* has continually been confused with *S. palmetto.* The two species are immediately distinguished by the number and spacing of major veins about the midvein in the leaf (Fig. 21). This character is best seen in fresh or rehydrated material viewed with transmitted light. The veins with bundle sheath extensions appear translucent; veins without bundle sheath extensions are not visible. *Sabal palmetto* has uniform spacing between the veins, while in *S. maritima,* the spacing is greatest around the midvein (Fig. 21). Near the margin or suture vein, the patterns of venation for the two species appear similar.

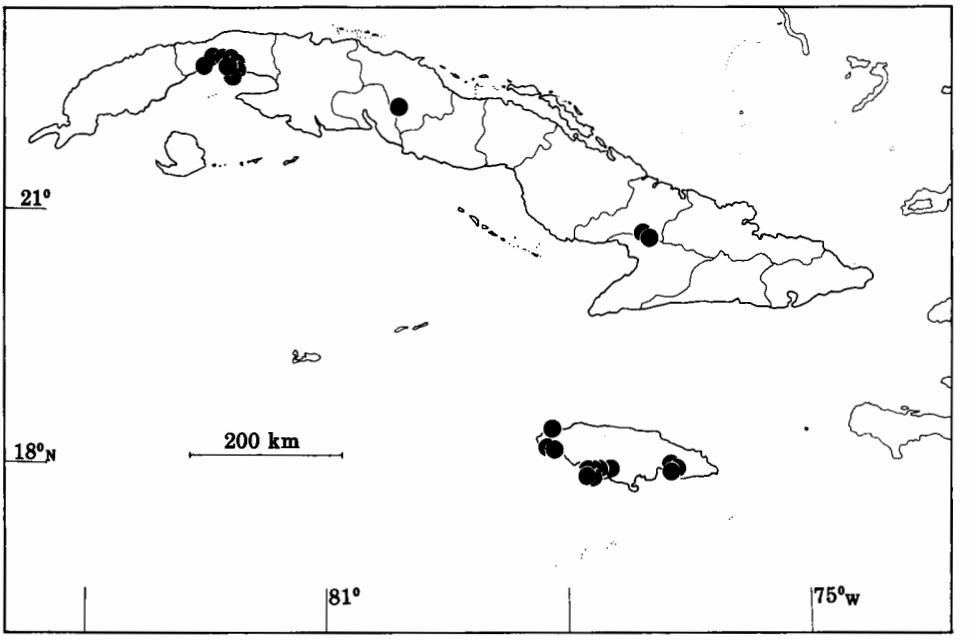

Fig. 20. Distribution of *Sabal maritima* in Cuba and Jamaica.

7. SABAL MAURITIIFORMIS (Karsten) Grisebach & H. Wendland in Grisebach, Fl. Brit. West Ind. 514. 1864. *Trithrinax mauritiaeformis* H. Karsten, Linnaea 28: 244. 1857.—Lectotype! [vide Glassman 1972*a*]: Karsten, Fl. colomb. 2: t. 172. 1866.

Sabal nematoclada Burret, Repert. Spec. Nov. Regni Veg. 48:256. 1940.—Type: "British Honduras: Forest Home, in woods," *Schipp S-443* [publ. as "*8443*"] (holotype: B).

Sabal allenii Bailey, Gentes Herb. 6:200. 1943.—Type: "Panama, Perlas Islands, Pedro Gonzales," 22 Nov 1941, *Allen 2604* (holotype: BH!).

Sabal morrisiana Bartlett ex Bailey, Gentes Herb. 6:412. 1944.—Type: "Guatemala: Peten, Uaxactun," 22 Mar 1931, *Bartlett 12284* (holotype: MICH!, fragment: BH!).

Sabal glaucescens Loddiges ex H. E. Moore, Gentes Herb. 9:287. 1963.—Type: "Trinidad, St. Patrick, Quinam Bay," 28 Jan 1946, *Bailey 119* (holotype: BH!).

Tall and slender palm to ca. 25 m tall; trunk 15–20 cm DBH, green and prominently ringed when young and aging to brown-gray. Leaves 15–25, evenly green or strongly glaucous, weakly costapalmate, not filiferous; petiole 2.2–3.2 cm wide, 2–3 m long; hastula acuminate or occasionally acute, 6.5–11 cm long, lepidote or glabrescent, margin of hastula revolute, erect, or involute and strongly ridged (esp. in Trinidad populations), entire or undulate; segments 90–120 per leaf, connate in groups of 2–3 for nearly their entire length (rarely solitary), the groups connate for only ca. 30% of their length, middle segment 125–200 cm long, 2.5–3.7 cm wide, 0.1 mm or less thick, transverse commissures prominent, abundant and long, apex bifurcate for 10–35 cm. Inflorescence ascending (becoming more or less arcuate in fruit) with 4 orders of branching, exceeding the leaves in length, sheathing bracts lepidote, rachillae 7–14 per branchlet, 0.5–1.1 mm in diameter, 4.5–6 cm long, with (8–)10–11(–13) flowers per cm. Flower 3.5–4.8 mm long; calyx cupulate or rarely urceolate, non- or only weakly costate when dry,

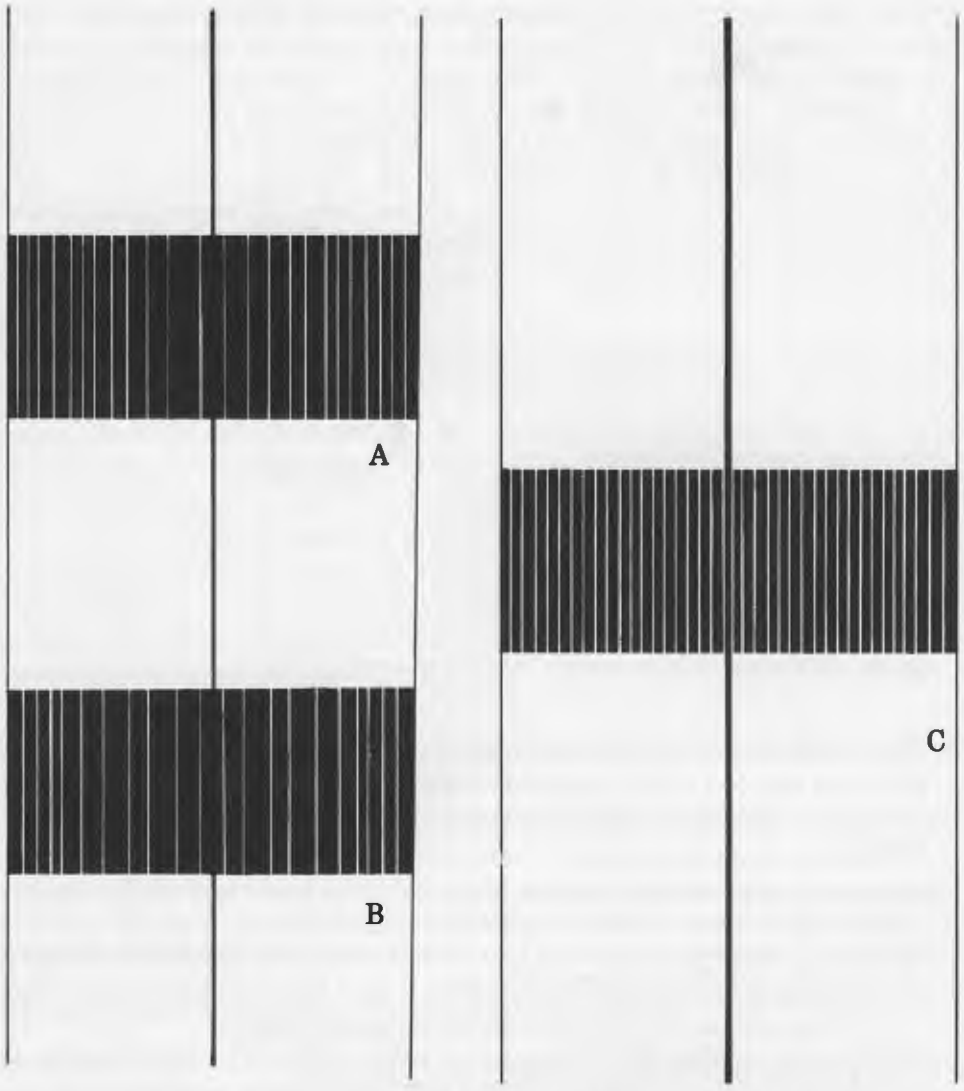

Fig. 21. Diagrammatic comparison of venation patterns of *Sabal maritima* and *S. palmetto*, living material viewed with transmitted light.—A. *S. maritima*, Cuba (*Zona 279*).—B. *S. maritima*, Jamaica (*Zona et al. 301*).—C. *S. palmetto*, Cuba (*Zona 280*).

1.4–2.4 mm long, 1.1–2.0 mm wide, sinuses 0.6–0.9 mm deep; petals ovate (rarely obovate), noncostate when dry, membranous, 2.4–3.9 mm long, 1.5–1.8 mm wide; antipetalous stamens spreading-reflexed, antisepalous stamens erect, filaments 2.7–3.5 mm long, basally connate and adnate to the corolla for 0.6–3.5 mm, anthers ca. 1.2 mm long and 0.6 mm wide; gynoecium 2.5–3.1 mm long, ovary 0.8–1.3 mm high, 0.8–1.1 mm in diameter. Fruit spherical to pyriform, blackish, 8.8–11 mm in diameter, 8.5–11 mm high; seed oblate spheroidal, 6.6–7.9 mm in diameter, 4.9–6.2 mm high, with rounded or bulging funicular remains; embryo supraequatorial or rarely equatorial. (Fig. 3E, 4C, 6B, 8G, 11C, 22.)

Fig. 22. *Sabal mauritiiformis* in Trinidad (*Zona & Ramkissoon 295*).

Representative specimens.—BELIZE. CAYO Dist.: Mountain Pine Ridge, San Agustín, *Lundell 6676* (MICH), *Lundell 6683* (MICH, NY); ca. 1 mi S of Belmopan, 0.5 mi E of Hummingbird Highway, *Spellman & Newey 1893* (MO).—STANN CREEK Dist.: Stann Creek Valley, on high ridge, *Gentle 3103* (BH, MICH).—COLOMBIA. Dept. ATLÁNTICO: Las Pendales, region of Barranquilla, *Elias 1550* (ECON).—Dept. BOLIVAR: vicinity of Turbaco, *Killip & Smith 14291* (A, NY).—Dept. LA GUAJIRA: Serranía de Santa María, S of Mingueo along road from Mingueo to San Antonio de Pueblo Viejo, *Gentry & Cuadros 47514* (MO, NY).—Dept. SUCRE: vicinity Coloso, alt. 300 m, *Gentry et al. 34843A* (MO).—Dept. VALLE: Mpio. Tolua, near Río Frío, *Gentry 54079* (MO).—COSTA RICA. Prov. LIMÓN: between Punta Manzanillo and Punta Mona, E of Manzanillo de Talamanca, *Grayum & Schatz 5253* (MO).—GUATEMALA. Dept. EL PETÉN: ruins of Tikal, *Moore & Cetto 8202* (BH).—MEXICO. CHIAPAS: Mpio. Ococingo, 4 km W of Crucero Corozal, *Martinez 6942* (RSA).—TABASCO: Mpio. Jalapa, Ranchería Aquiles Serdán, between Villahermosa and Escárcega, 1 km before road to Cacao oil fields, *Zona et al. 141 & 142* (RSA); Mpio. Villahermosa, between Villahermosa and Escárcega, *Cowan & Zamudio 3350* (MO, NY).—OAXACA: Distr. Tehuantepec, isthmus road beyond Matias Romero ca. 37 mi from Empalme Balboa, *Moore & Brossard 6350* (BH).—VERACRUZ: Mpio. Jesús Carranza, Nuevo Morelos, *Moore 8112* (BH).—PANAMA. Without locality, *Duke 14307* (MO).—Prov. DARIÉN: Santa Fe, *Duke 8395* (MO); near Santa Fe, *Duke 12286(2)* (BH).—Prov. PANAMÁ: along Pan American Highway between El Llano and Río Mamoní, *Duke 5646* (MO); 2 mi E of Río Mamoní along Pan American Highway, *Zona et al. 264* (RSA); near dam site S of Canita, *Croat 14513* (MO); El Congrejal, vicinity of La Jagua, *Bartlett & Lasser 17021* (MICH).—TRINIDAD. Hearts Cut to Belle View, *Britton 2237* (NY); Caroni Co., distr. Montserrat, between Caparo and Flannigan Town, *Zona & Ramkissoon 295* (RSA); St. Patrick Co., dist. La Brea, between Guapo and Pt. Ligoure, *Zona & Ramkissoon 296* (RSA); Roussillac, *Zona & Ramkissoon 297* (RSA); Victoria Co., San Fernando Hill, *Britton & Hazen 1052* (GH, NY).—VENEZUELA. Esto. BARINAS: near La Libertad, *Bernardi 1176* (MO).—Esto. BOLIVAR: Hato la Vergarena, E of Cerro Coroba, *Wurdack & Guppy 133* (NY); Represa Guri, ca. 65 km NE of Ciudad Piar, *Liesner & Gonzales 11184* (MO).—Esto. ZULIA: Sierra de Perija, near Kasmera (Estacion Biol. de la Univ. de Zulia), SW of Machiques, *Steyermark & Fernández 99744* (MO); distr. Mara, near Río Guarsare, between Rancho 505 and Cerro Yolanda, *Steyermark et al. 122871* (MO, NY).—Between Esto. FALCÓN and Esto. LARA: Cerro Socopo, *Liesner et al. 8454* (MO).

Common names.—Botan, carat, carata, palma amarga, palma de guagara, palma de vaca.

Distribution and ecology (Fig. 23).—The distribution of this species is noteworthy for its patchiness. It occurs abundantly in isolated populations in southern Mexico, Belize and Guatemala, extreme southeastern Costa Rica, eastern Panama and the Perlas Is. in the Bay of Panama, north coastal South America (Colombia and Venezuela) and Trinidad. It grows at elevations up to 1000 m but is generally found at 0–400 m, often on soils derived from limestone.

Sabal mauritiiformis is encountered in both rain forest and secondary growth. In pastures and other anthropogenic habitats it is associated with *Scheelea liebmannii* Becc. (Mexico), *Tectonia grandis* L. f. (introduced) and *Cavanillesia platanifolia* (Humb. & Bonpl.) HBK (Panama), and *Swietenia* sp. (Venezuela).

Phenological records for *Sabal mauritiiformis* show that it flowers from March to October, but flowering is probably sporadic throughout the year.

Discussion.—Dahlgren (1936) suggested *Karsten s.n.* as a type of *Trithrinax mauritiaeformis* without specifying the location of this specimen. Until this specimen can be located, I follow Glassman's (1972*a*) choice in lectotype: the excellent illustration in t. 172 of Karsten's 1866 publication.

This is a highly specialized species with many unusual morphological and anatomical characters, such as stomata on only one surface of the leaves, leaf segments thin and clustered, ascending inflorescences, four orders of branching,

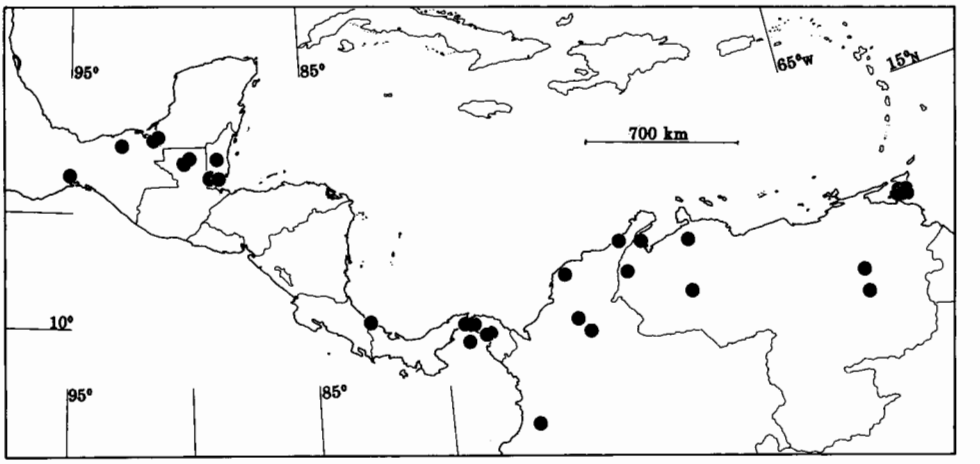

Fig. 23. Distribution of *Sabal mauritiiformis*.

and rather short rachillae. Although it resembles *S. yapa* superficially, *S. mauritiiformis* is clearly distinct anatomically, morphologically, and ecologically.

8. SABAL MEXICANA Martius, Hist. nat. palm. 3:246, t. 8. 1839. *Inodes mexicana* (Mart.) Standley, Contr. U.S. Nat. Herb. 23:71. 1920.—Type: "Mexico, Oaxaca," 1832, *Karwinski s.n.* (lectotype [vide Glassman 1972*a*]: M, fragment FI! MO!, photograph: FI! NY!).

Sabal texana (Cook) Beccari, Webbia 2:78. 1907. *Inodes texana* Cook, Bull. Torrey Bot. Club 28: 534. 1901.—Type: "Banks of the Rio Grande below Brownsville, Texas," 1890, *Stark s.n.* (lectotype [vide Glassman 1972*a*]: A!).

Sabal exul (Cook) Bailey, Rhodora 18:155. 1916. *Inodes exul* Cook, U.S.D.A. Bur. Pl. Ind. Cir. 113:14. 1913.—Type: "Texas, the lawn of Mrs. Martin O'Connor, Victoria," without date, *Cook s.n.* (holotype: US!).

Robust palm to ca. 15 m tall; trunk 20–35 cm DBH, gray, with or without leafbases. Leaves 10–25?, evenly green, strongly costapalmate, filiferous; petioles 2.9–3.2 cm wide, ca. 1–2 m long, hastula acuminate to acute, 9.5–15.5 cm long, glabrous or glabrescent, margin of hastula erect and undulate, occasionally entire or strongly involute and ridged; segments 80–115 per leaf, connate for ca. 30% of their length, middle segment 80–145 cm long, 3.2–5.3 cm wide, 0.2–0.4 mm thick, transverse commissures abundant, long and conspicuous (very rarely inconspicuous), apex bifurcate for 20–40 cm. Inflorescence arcuate with 3 orders of branching, equalling the leaves in length, sheathing bracts lepidote or glabrescent, rachillae 7–27 per branch, 0.8–1.6 mm in diameter, 5.5–14 cm long, with (8–) 10(–12) flowers per cm. Flower 3.7–6.5 mm long; calyx cupulate, strongly costate when dry, 1.8–2.7 mm long, 1.3–2.1 mm wide, sinuses 0.4–1.2 mm deep; petals obovate, costate when dry (apparent even in mature buds), membranous, 3.1–4.9 mm long, 1.0–2.3 mm wide; stamens ascending-spreading, filaments 3.2–4.9 mm long, adnate to the corolla for 0.7–2.1 mm, anthers ca. 1.4 mm long and 0.7 mm wide; gynoecium 2.5–4.0 mm long, ovary 0.6–1.8 mm high, 0.6–1.2 mm in diameter. Fruit spherical to oblate-spheroidal, black, with a thick pericarp, 14.8–

19.3 mm in diameter, 13.8–17.0 mm high; seed oblate concave, 8.6–13.3 mm in diameter, 5.4–7.4 mm high, with smooth or protruding funicular remains; embryo supraequatorial, rarely equatorial. (Fig. 6C, 8H, 11D, 24.)

Representative specimens.—EL SALVADOR. Dept. SAN VINCENTE: near Estero de Jaltepeque, *Allen 6897* (NY).—MEXICO. GUERRERO: Mpio. Tecpan, San Pedro, *Langlassé 60* (GH, MO, P); San Luis, *Langlassé 826* (GH, P).—OAXACA: without locality, Nov 1842, *Liebmann 10807* (GH, MO, P); Mpio. Juchitán de Zaragoza, La Ventosa, *Zona et al. 221* (RSA); 6 km E of La Ventosa, *Zona et al. 222* (RSA).—SAN LUIS POTOSÍ: Mpio. San Antonio, San Antonio, *Alcorn 2746* (NY).—TAMAULIPAS: without locality, *Bartlett 11106* (A, GH, MO); Mpio. Matamoros, vicinity of Matamoros, *Berlandier 877* (GH), *Berlandier 2307* (FI, GH, MO, NY); Mpio. Tampico, vicinity of Tampico, 27–30 Apr 1910, *Palmer s.n.* (GH, NY); Mpio. Cd. Victoria, vicinity of Cd. Victoria, *Palmer 193* (CM, GH, MO, NY).—VERACRUZ: Mpio. Alvarado, La Tunilla, near Puente Tlacotlapán, *Zona et al. 140* (RSA); Mpio. Tierra Blanca, between Cd. Alemán and Tierra Blanca, *Zona et al. 147* (RSA); Mpio. Medellín, Rancho "La Laguna," *Zona et al. 138* (RSA); Mpio. Naolinco, near Paso del Toro, *Pennington & Sarukhán 9585* (A); Mpio. San Andrés Tuxtla, 3 km N of Salinas, *Nevling & Gomez-Pompa 93* (GH); Mpio. Tantoyuca, near Wartenberg, *Ervendberg 314* (GH, P).—YUCATÁN: Mpio. Maxcanu, Maxcanu, *Zona et al. 145* (RSA). U.S.A. TEXAS: Cameron Co., banks of Rio Grande below Brownsville, 9 Apr 1887, *Sargent s.n.* (A, GH); S of Brownsville, *Lundell & Lundell 8700* (MICH); Las Palmas Ranch, *Ferris & Duncan 3199* (MO, NY); near Southmost, *Webster & Wilbur 3022* (MICH); Victoria Co., Victoria, cultivated, *Bailey 715* (BH) and *13174* (BH).

Common names.—Palma llanera, palma de micharo, palma real, palma redonda, palma rustica, soyate, guano, bouxaan, xaan, otoomal, and many others (see Piña 1972).

Distribution and ecology (Fig. 19).—*Sabal mexicana* is distributed in extreme southern Texas, much of gulf coastal Mexico, Oaxaca, and the Yucatan Peninsula. A single collection is known from El Salvador.

Its presence in Yucatán may be attributed to the activities of pre-Columbian peoples (J. Caballero pers. com.). In Yucatán, it is grown in plantations and is the mainstay of the thatch industry (Fig. 24).

Common associated species are *Bursera simaruba* Sarg., *Lysiloma divaricatum* (Jacq.) Macbr., *Pithecellobium brevifolium* Benth., *Cedrela mexicana* Roem., *Crescentia alata* Kunth, *Scheelea liebmannii* Becc., and various species of *Acacia.* A full account is given by Piña (1972).

This species is most often collected with flowers during the early part of the year, January through May, but a few specimens with flowers are known from other months as well.

Discussion.—*Sabal mexicana* is one of the most common palms of lowland tropical Mexico. It is a weedy species widespread in disturbed and anthropogenic habitats. Its closest relative, *S. guatemalensis,* shares similar habitats in southern Mexico; however, their sympatry may be secondary, the result of human activity. Increasing aridity in the isthmus of Tehuantepec or Tehuacán valley may have bisected a formerly widespread ancestral species. *Sabal mexicana,* with its xeromorphic anatomical adaptations, probably arose in the cooler and drier areas north of the Tehuacán valley, and *S. guatemalensis,* the more mesomorphic of the two, probably arose in the more humid areas to the south.

9. SABAL MIAMIENSIS Zona, Brittonia 37:366. 1985.—Type: "Florida, Coconut Grove," 2, 5 Nov 1901, *Small and Nash s.n.* (holotype: NY!; isotypes: BH! F! US!).

Fig. 24. Young leaves of *S. mexicana* harvested for fiber in Yucatán, Mexico. Note roof of *Sabal* thatch.

Understory palm with an underground stem. Leaves 3–6, evenly green, strongly costapalmate, filiferous or not; petiole 1.5–3.0 cm wide and 0.4–0.6 m long; hastula acute, 2.4–7.7 cm long, glabrous, margin flat or erect, entire; segments 35–70 per leaf, connate for ca. 20% of their length, middle segment ca. 85 cm long, 2.8–3.0 cm wide, 0.2–0.3 mm thick, transverse commissures short and conspicuous, apex bifurcate for 21–38 cm. Inflorescence arcuate with 3 orders of branching, equal to or exceeding the leaves in length, sheathing bracts lepidote, rachillae 18–20 per branchlet, ca. 1.0 mm in diameter, 14–15 cm long, with ca. (3–)5(–7) flowers per cm. Flower 5.0–5.5 mm long, calyx urceolate-cupulate, strongly costate when dry, 1.6–2.0 mm long, 1.5–2.0 mm wide, sinuses ca. 0.5 mm deep; petals obovate, noncostate when dry, membranous, 3.7–4.7 mm long, 1.7–2.0 mm wide; stamens spreading, filaments 4.0–5.0 mm long, adnate to the corolla for 1.0–1.4 mm, anthers ca. 1.6 mm long and 0.7 mm wide; gynoecium 3.2–3.7 mm long, ovary 0.7–1.2 mm high, 0.8–1.1 mm in diameter. Fruit oblate, black, with a very thick pericarp, 15.7–19.0 mm in diameter, 14.3–16.9 mm high; seed oblate concave, 10.2–11.0 mm in diameter, 6.2–6.7 mm high; embryo supraequatorial. (Fig. 6D, 9A, 12A.)

Representative specimens.—U.S.A. FLORIDA: Broward Co., Ft. Lauderdale, 19, 25 Nov 1903, *Small and Carter s.n.* (FLAS, US); Ft. Lauderdale, 8 Aug 1935, *Bailey and Hume s.n.* (FLAS); Dade Co., Miami, Nov 1904, *Small s.n.* (FLAS, NCU, US); *Small and Carter 1294* (NY, US); Miami, "Mr. Mosear's place," 16 Apr 1932, *Cook and Presley s.n.* (US); 27 Apr 1932, *Cook and Presley s.n.* (BH); Buena Vista, N of Miami, *Small 6240* (BH); Interama, *Avery 1575* (FLAS).

Common name.—Miami palmetto.

Distribution and ecology (Fig. 25).—This species is endemic to the Miami Pinelands of southern Florida, near sea level, on outcroppings of oolitic limestone known as the Everglades Keys. *Sabal miamiensis* occurs with *Byrsonima lucida* (Turcz.) P. Wilson, *Guettarda scabra* Vent., *Metopium toxiferum* (L.) Krug & Urban, *Pinus elliottii* Engelm. var. *densa* Little & Dorman, *Quercus geminata* Small, *Serenoa repens* (Bartram) Small, *Tetrazygia bicolor* (Mill.) Cogn., and *Zamia pumila* L., among others (Harper 1927).

Herbarium records are scant, but collections with flowers are known from throughout the year.

The species was proposed for listing as an Endangered Species by the U.S. federal government; however, the proposal was withdrawn owing to disagreement concerning the validity of the taxon. Federal protection, however, would be in name only, as the species is likely already extinct. Its habitat in Dade County has been urbanized and utterly destroyed.

Discussion.—The taxonomic history of this species has been given elsewhere (Zona 1983, 1985). The presence of both dwarfed *S. palmetto* and *S. etonia* in south Florida undoubtedly has led to some confusion which in turn has contributed to the debate concerning the validity of this taxon. Undoubtedly, *S. miamiensis* is more closely related to *S. etonia* than was previously believed (Zona 1985). Anatomically, *S. miamiensis* shares many features with *S. etonia*; although, *S. etonia* has more adaptations to arid environments. The morphological characteristics given previously (Zona 1985) are still useful in distinguishing the species, i.e., lax arching inflorescence with three orders of branching and large fruits and seeds. The fruits of *S. miamiensis* are 15.7–19.0 (16.9 ± 1.1) mm in diameter, versus 9.0–15.4 (12.9 ± 1.9) mm in *S. etonia*. Habitat differences are critical.

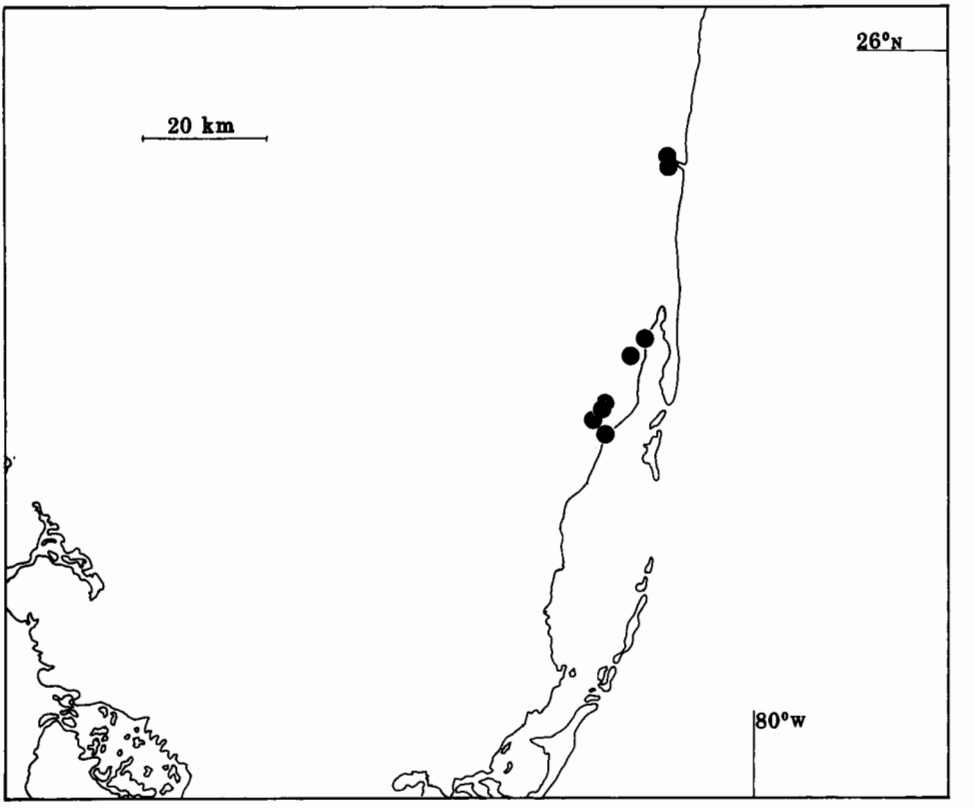

Fig. 25. Distribution of *Sabal miamiensis* in southeastern Florida.

Sabal etonia has often been confused with *S. miamiensis,* but the former grows on white sand, not oolite. The above description of flowers is based on only two specimens and probably does not fully account for all the variation in this species.

10. SABAL MINOR (Jacq.) Persoon, Synops. Pl. 1:399. 1805. *Corypha minor* Jacquin, Hort. bot. vindob. 3:8, t. 8. 1776. *Sabal adansonii* Guersent, Bull. Sci. Soc. Philom. Paris 3:206. 1804.—Type: "Hort. Vindob.," *Jacquin s.n.* (holotype: BM!).

Sabal pumila (Walt.) Elliott, Sketch bot. S. Carolina 1:430. 1817. *Corypha pumila* Walter, Fl. Carol. 119. 1788. *Chamaerops acaulis* Michaux, Fl. Bor.-amer. 1:207. 1803.—Type, designated here: "South Carolina, St. Andrews," May 1855, *Hexamer & Maier* (neotype: GH!; isoneotype: CM!).

Rhapis arundinacea Aiton, Hortus Kewensis 3:474. 1789.—Type: "Hort. Kew, Florida oriental," 1777, without collector (holotype [vide Moore 1975]: BM).

Rhapis acaulis Walter ex Willdenow, Sp. Pl. 4:1093. 1805 [publ. 1806].—Type: B-Willd. not seen.

Sabal louisiana (Darby) Bomhard, J. Wash. Acad. Sci. 25:35, 44. 1935. *Chamaerops louisiana* Darby, Geogr. Descr. Louisiana 194. 1816.—Type: unknown, may be at BH.

Sabal ? *adiantinum* Rafinesque, Fl. ludov. 17. 1817.—Type: unknown, may be at P-DU.

Sabal minima Nuttall, American Jour. Sci. ser. 1: 5:293. 1822. *Brahea minima* (Nutt.) H. Wendland in Kerchove, Palm. 235. 1878.—Type: "Florida," *Ware s.n.* (holotype: unknown, may be at BM).

Chamaerops sabaloides Baldwin ex W. Darlington, Reliq. baldw. 334. 1843.—Type: unknown, may be at PH.

Sabal deeringiana Small, Torreya 26:34. 1929.—Type: "Louisiana. Lake Pontchartrain," 10 Apr 1925, *Small and Cocks s.n.* (holotype: NY, not located).

Sabal adansonii Guersent var. *major* hort. ex Beccari, Ann. Roy. Bot. Gard. (Calcutta) 13:291. 1931 [publ. 1933].—Type: unknown, may be at FI.

Small understory palm to 3 m tall (rarely taller); trunk usually subterranean but may emerge to ca. 2 m, 10–20 cm in diameter. Leaves 4–10, dark green, weakly costapalmate, usually not filiferous; petiole 0.5–2.6 cm wide, 0.3–0.9 m long; hastula obtuse, 0.8–4.7 cm long, glabrous or rarely glabrescent, margin flat and entire but occasionally erect or undulate; segments 15–65 per leaf, connate for ca. 20% of their length, blade typically divided into two equal halves by a deep division at the apex of the leaf, middle segment 34–84 cm long, 1.4–3.7 cm wide, 0.2–0.4 mm thick, transverse commissures short, straight, infrequent, and conspicuous, apex bifurcate for 0–15 cm, usually entire. Inflorescence erect, exceeding the leaves in height, with 2 (rarely 3) orders of branching, main axis with long internodes giving the inflorescence a very open and simple appearance, sheathing bracts lepidote or glabrous, rachillae 7–27 per branchlet, 0.8–1.1 mm in diameter, 4–14 cm long, with (5–)6–7(–8) flowers per cm. Flower 3.5–5.2 mm long, calyx campanulate to urceolate, strongly costate when dry, 1.4–2.2 mm long, 1.2–1.7 mm wide, sinuses 0.4–0.8 mm deep; petals ovate-obovate, noncostate when dry, membranous, 2.7–3.5 mm long, 1.5–2.1 mm wide; stamens ascending to spreading, filaments 2.7–4.1 mm long, adnate to the corolla for 0.5–1.7 mm, anthers ca. 0.9 mm long and 0.6 mm wide; gynoecium 2.0–3.0 mm long, ovary 0.5–1.0 mm high and 0.1–1.1 mm in diameter. Fruit oblate spheroidal to spherical, brown to black, with a thin papery pericarp, 6.4–9.7 mm in diameter, 6.2–8.5 mm high; seed oblate spheroidal, 4.4–6.9 mm in diameter, 3.5–5.1 mm high, often with a small funicular beak; embryo equatorial, rarely supra- or subequatorial. (Fig. 3A, 6E, 9B, 11E.)

Representative specimens.—U.S.A. ALABAMA: Mobile Co., Dauphin Island, *Deramus D947* (MO); Tuscaloosa Co., swamp of Big Sandy Creek near Duncanville, *Harper 3281* (GH, MO).—ARKANSAS: Clark Co., near Gurdon, *Demaree 21773* (MO); Desha Co., NW of Dumas, 3 Sep 1936, *Wherry s.n.* (GH); Drew Co., near Ozmont, *Demaree 13711* (GH, MO); Little River Co., Red River Bottoms near Alleene, *Demaree 64376* (MO); Miller Co., McKinney Bayou bottoms near Texarkana, *Demaree 24494* (MO); woods opposite Fulton, *Palmer 22271* (A, P); Phillips Co., near Huma, 23 Jul 1896, *Eggert s.n.* (MO); Ouachita Co., near Camden, *Demaree 37614* (GH).—FLORIDA: Alachua Co., Gainesville, University of Florida campus W of Hume Hall, *Perkins & Herring 987* (RSA); Citrus Co., *Hitchcock 1999* (F); Columbia Co., Lake City, *Rolfs 703* (F); Duval Co., near Jacksonville, *Curtis 5784* (GH, GA, MO, NY, P); Hernando Co., 0.1 mi W of Spring Lake on Old Spring Lake Rd., *Thompson & Nishida 2901* (CM); Hillsborough Co., Hillsborough River State Park, *Lakela 26375 et al.* (RSA); Lake Co., Orange Bend, *Nash 1871* (A, NY); vicinity of Eustis, *Nash 836* (F, GH, MICH, NY, P); Manatee Co., *Garber 51* (CM, GH); Okaloosa Co., Choctawhatchee Bay at Sardine Lake, *Davis 11691* (CM); Polk Co., Faulkner Hammock, *McFarlin 6640a* (MICH); vicinity of Kissenger Springs, *McFarlin 3060* (MICH); near Barstow, *McFarlin 5927* (MICH); Peace River, NE of Ft. Meade, 1 Jan 1920, *Jennings s.n.* (CM); Santa Rosa Co., near Milton, *Rolfs 669* (F, GA, MO); Sumter Co., Indian Field ledges E of Withlacoochee River, *Lakela 26449 & 26452* (GH).—GEORGIA: Bulloch Co., Ogeechee River, 15 mi E of Statesboro, *Nutting 151* (RSA); Charlton Co., Okefenokee National Wildlife Refuge, Billy's Is., *Newcombe 260* (RSA); Early Co., SE of Blakely, *Utech & Ohara 83-357* (CM); Emanuel Co., N of Oak Park, *Boufford et al. 21680* (CM); McDuffie Co., vicinity of Thomson, *Bartlett 1441* (MICH); McIntosh Co., near Darien, *Smith 2096* (F); Sumter Co., woods near Flint River, *Harper 1055* (MO, NY); Thomas Co., near Ochlockonee River, 12–22 Jul 1895, *Small s.n.* (F, NY).—LOUISIANA: Cameron Parish, Rockefeller Foundation Wildlife Refuge, *Boufford 10286* (CM); Claiborne Parish, Sugar Creek Valley, *Moore & Moore 6768* (GH); East Baton Rouge Parish, 5 mi S of University Bayou Foutain, *Brown 1483* (MICH); Iberia Parish, Avery Is., *Correll & Correll 9565* (GH); Jefferson Parish, Black Bayou swamplands, *Ewan 18317* (GH); near Westwego, *Ewan 17444* (MO); Livingston Parish, 0.5 mi N of French Settlement, *Miller 10* (MO); Colyell Bay, E end of Port Vincent, *DeBuhr*

& Wallace 2315 (RSA); Orleans Parish, Fort Macomb, Chef Menteur, *Ewan 18740* (MO, GH); Rapides Parish, vicinity of Alexandria, *Ball 452* (CM, F, GH, MO); St. John the Baptist Parish, near shore of Lake Pontchartrain, *Ewan 20374* (GH); hammock near Frenier, 12 Sep 1929, *Small s.n.* (A, MICH, NY, USF); St. Martin Parish, 19 Apr 1927, bayou banks S of Morgan City, *Small et al. s.n.* (NY).—MISSISSIPPI: Harrison Co., Biloxi, *Tracy 3588* (NY) & *5145* (F, MO, NY); Sharkey Co., Panther Creek area of Delta Purchase Unit near Sartartia, *Ray 4917* (GH); Tallahatchie Co., 12 mi S of Charleston, *Hardin 454* (GH, MICH).—NORTH CAROLINA: Craven Co., Slocum Creek near New Berne, 29 Jul 1927, *Abbe & Spalteholz s.n.* (BH); Dare Co., near Wilmington, *Williamson 64* (CM); New Hanover Co., Fort Fisher on the Lower Cape Fear Peninsula, *Godfrey 6184* (GH); Onslow Co., Adler's Is., White Oak River, NE of Swansboro, *Wood 6397* (GH); Pender Co., 6 mi N of Burgaw, *Godfrey 6517* (GH).—OKLAHOMA: McCurtain Co., 2 mi S of Tom, *Waterfall 12417* (GH); 9 mi SW of Haworth, *Nelson et al. 5408* (GH, MO, RSA).—SOUTH CAROLINA: Berkely Co., Palmer Bridges, 5 mi ESE of Honeyhill, *Godfrey & Tryon 131* (F, GH, MO); Charleston Co., 8 mi W of Charleston, *Wiegand & Manning 664* (RSA); Georgetown Co., 12 mi N of Georgetown, *Godfrey & Tryon 89* (F, MO).—TEXAS: Brazoria Co., 1.9 mi NE of FR 524 on FR 521, *Thompson & Rawlins 504* (CM); 11 mi SW of Alvin, Chocolate Bayou, *Cory 51037* (MICH); Dallas Co., 4 air mi SW of Seagoville, 1.25 mi NE of Trinity River at start of Parsons Slough, *Cory 53836* (MICH); Galveston Co., end of Oak Lane, extreme N side of Alta Loma, *Waller & Bauml 3231* (GH, MO); Hardin Co., N of Sour Lake, *Lundell & Lundell 10878 & 11552* (MICH); 6 mi NW of Saratoga, 31 May 1962, *Boardman s.n.* (CM); Harris Co., Houston, *Hall 616* (F, GH, MO, NY); 50 yds N of Buffalo Bayou in Houston Memorial Park, *Traverse 128* (GH); Jackson Co., Menehee Flats S of Vanderbilt, *Tharp & Barkley 13A100* (GH, MO); Kaufman Co., 5 air mi ESE of Combine, E fork of Trinity River, *Cory 52557* (GH, MICH); Kendall Co., Spanish Pass, *Palmer 9871* (A, P) and *10840* (A, MO); near Boerne, Spring Creek, *Palmer 12245* (A, GH); Polk Co., 15 mi N of Livingston, *Hamby 1743* (RSA); Wharton Co., East Bernard Creek, *Ferris & Duncan 3259* (MO, NY).

Common names.—Bush palmetto, dwarf palmetto, little blue stem, swamp palmetto (Alabama, Florida, Georgia), latania and latanier (Louisiana).

Distribution and ecology (Fig. 26).—*Sabal minor* has a wide distribution in the southeastern United States and is the most northernly ranging species in the genus. Throughout its range, it is a palm of the rich soils of floodplains, levees, river banks, and swamps where it is associated with broadleaf deciduous trees of genera such as *Acer, Betula, Carpinus, Carya, Celtis, Crataegus, Ilex, Liquidambar, Quercus,* and *Ulmus.* Nixon, Chambless, and Malloy (1973) present a detailed ecological study of *S. minor* in Texas.

Like other north temperate species of *Sabal, S. minor* shows strong seasonality in flowering. It blossoms in the warm months of April through August, with peak activity in June.

Discussion.—*Sabal minor* has a most colorful taxonomic history. It is a conspicuous element of the vegetation of the southeastern United States and is relatively easy to collect and press, so *S. minor* was included, under various names, in the floras of nearly every early American and European botanist.

Glassman (1972*a*) designated plate 8 of Jacquin's publication as the lectotype; however, a specimen (2 sheets) deposited at BM and bearing labels in Jacquin's own hand (D'Arcy 1970) appear to satisfy the definition of holotype.

The species is highly variable, and most troublesome to early botanists was the presence or absence of an above ground stem. Palms of this species with conspicuous aerial stems have been described as *S. louisiana* and *S. deeringiana.* At the western edge of its range, *S. minor* is often arborescent and large, but over the entirety of its range, the species varies along a continuum in both size and arborescence. Furthermore, plants of *S. minor* growing in rich soils can attain unusually large dimensions, but this variation in size appears to be environmen-

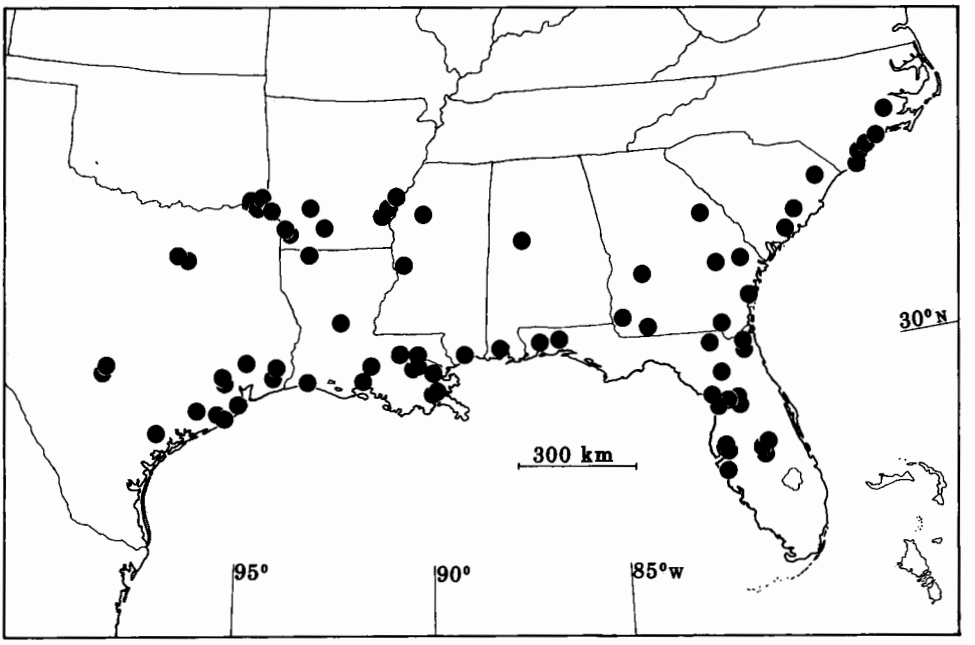

Fig. 26. Distribution of *Sabal minor*.

tally induced. Since the arborescent individuals have not been shown to be genetically isolated from the suffrutescent individuals, I treat both as variants of a single variable species.

The erect, sparsely branched inflorescence, with two(–three) orders of branching and long internodes between branches on the primary axis, the usually nonbifid leaf segment apices, and small fruits reliably separate this widespread species from its congeners.

11. SABAL PALMETTO (Walt.) Loddiges ex J. A. & J. H. Schultes. Syst. veg. 7:1487. 1830. *Corypha palmetto* Walter, Fl. Carol. 119. 1788. *Chamaerops palmetto* (Walt.) Michx., Fl. bor.-amer. 1:206. 1803. *Inodes palmetto* (Walt.) Cook, Bull. Torrey Bot. Club 28:532. 1901.—Neotype, designated here: "Florida, near Jacksonville," Jul, *Curtis 2677* (neotype: NY!: isoneotypes: BH! F! GA! GH! MICH! MO! US!).

Inodes schwarzii Cook, Bull. Torrey Bot. Club 28:532. 1901.—Type: "Florida, south of Coconut Grove," without date, *Cook s.n.* (holotype: US, not located).

Sabal palmetto var. *bahamensis* Beccari, Webbia 2:38. 1907. *Sabal bahamensis* (Becc.) Bailey, Gentes Herb. 6:417. 1944.—Type: "Bahama Islands, New Providence, along north side of Lake Killarney," 3 Mar 1888, *Eggers 4360* (lectotype, designated here: C, Field Museum neg. 21121, photograph: NY! RSA!).

Sabal parviflora Beccari, Webbia 2:43. 1907.—Type: "Cuba," without date, *Wright 3970* (holotype: B [destroyed], fragment: FI!; isotypes: A! NY! P! US!).

Sabal jamesiana Small, J. New York Bot. Gard. 28:182. 1927.—Neotype, designated here: "Florida, Deering Hammock," 26 Aug 1929, *Small and Mosier s.n.* (NY!).

Sabal viatoris Bailey, Gentes Herb. 6:403. 1944.—Type: "California, cultivated at Huntington Botanical Garden, San Marino," 2 Mar 1927, *Bailey 9248* (lectotype, designated here: BH!).

Stocky to emergent palm to ca. 20 m tall; trunk ca. 20–35 cm DBH, brown to gray. Leaves 15–30, evenly green, strongly costapalmate, generally filiferous; pet-

iole 2.2–4.2 cm wide and 1–2 m long; hastula acute to acuminate 5.3–18.0 cm long, lepidote or glabrescent, margins of hastula erect and undulate, or flat or entire, rarely revolute; segments 50–95 per leaf, connate for ca. 35% of their length, middle segment 55–120 cm long, 2.5–4.2 cm wide, 0.2–0.4 mm thick, transverse commissures conspicuous and short or obscure, apex bifurcate for 16–62 cm. Inflorescence arcuate with three orders of branching, nearly equalling to slightly exceeding the leaves in length, sheathing bracts usually lepidote, rachillae 9–22 per branchlet, 0.8–1.4 mm in diameter, 4–13.5 cm long, with (5–)7–8(–9) flowers per cm. Flower 4.1–6.7 mm long; calyx cupulate to cupulate-urceolate, strongly costate when dry, 1.3–2.4 mm long, 1.4–2.1 mm wide, sinuses 0.5–1.0 mm deep; petals obovate to spatulate, noncostate when dry, membranous, 3.1–4.8 mm long, 1.4–2.5 mm wide; stamens spreading, filaments 3.0–5.1 mm long, adnate to the corolla for 1.0–1.6 mm, anthers ca. 1.4 mm long and 0.7 mm wide; gynoecium 2.7–4.0 mm long, ovary 0.7–1.3 mm high, 0.7–1.1 mm in diameter. Fruit spherical or somewhat oblate pyriform, black, with a medium thick pericarp, 8.1–13.9 mm in diameter, 8.0–13.8 mm high; seed oblate, 5.4–9.7 mm in diameter, 4.0–7.0 mm high, occasionally with a small protruding funicular remnant; embryo supraequatorial, very rarely equatorial. (Fig. 2, 7A, 9C, 12B, 21C, 27.)

Representative specimens.—BAHAMAS. Andros Island, Loggerhead Creek region, *Bailey 1024* (BH); Bimini, South Bimini, *Howard & Howard 10170* (GH, NY); Eleuthera, Harbour Island, *Britton 6441* (F, NY); Exumas, Hummingbird Cay, *Nickerson et al. 2890* (A, MO); Hog Island, *Eggers 4114* (NY); Inagua, Smith's Thatch Pond (Lantern Head Pond), *Proctor 11741* (A); Mayaguana, *Gillis & Proctor 11646* (A); New Providence, *Cooper & Cooper 31* (GH); Prospect Hill region, *Bailey 1001* (BH); Salt Key Bank, Salt Key, *Wilson 8088* (F, NY).—CAICOS ISLANDS. North Caicos, Bellemont, *Millspaugh & Millspaugh 9186* (F, NY).—CUBA. ISLA DE LA JUVENTUD (Isla de Pinos): Mpio. Nueva Gerona, near Nueva Gerona, *Curtiss 484* (A, BH, CM, GH, MO, P); 1.5 mi E of Nueva Gerona, *Jennings 70* (CM).—LA HABANA: Jardín Botánico Nacional, cultivated, *Zona 280* (RSA); Mpio. Guira de Melena, N of Playa de Cajio, *León 14702* (GH); Mpio. Madruga, La Jíquima hill, *León 14685* (GH); N of Madruga, *Britton et al. 782* (CM); Mpio. Batabanó, Peralta, *León 14575* (GH).—MATANZAS: Mpio. Matanzas, mouth of the Canimar River, *Britton et al. 567* (CM); Mpio. Varadero, Península de Hicacos, *Acuña 14901* (BH).—SANCTI SPIRITUS (Las Villas), Mpio. Sancti Spiritus, Guasimal, *León 14682* (GH).—U.S.A. FLORIDA: Alachua Co., S of Gainesville, S side of Alachua Sink, *Easterday 912* (FLAS); Brevard Co., Indian River 8 mi S of Melbourne, 8 Aug 1935, *Hume s.n.* (FLAS); Broward Co., Ft. Lauderdale, *Bailey 59* (BH); Citrus Co., 1.8 mi N of Homasassa, *Baltzell 7171* (FLAS); Collier Co., Marco, *Standley 12689* (US); Dade Co., Opa Locka, hammock, 5 Sep 1929, *Small & Mosier s.n.* (BH, NY); Duval Co., fields near Jacksonville, *Curtiss 4987* (F, GA, GH, NY, US); Gulf Co., shore of Gulf at St. Joe, 4 Apr 1933, *Bailey & Bailey s.n.* (BH); Hernando Co., ca. 6 mi ENE of Brooksville, *Lakela 25294* (USF); Highlands Co., edge of Lake Josephine, near Sebring, *McFarlin 6037* (MICH); Hillsborough Co., 0.8 mi from Polk County line on Hwy 60, *Lakela 23945* (USF); Indian River Co., Indian Lane, Indian River Shores, *D'Arcy 2873* (FLAS); Lake Co., vicinity of Eustis, *Nash 1164* (F, GH, MICH, MO, NY, US); Lee Co., western Sanibel Island, *Brumbach 8457* (FLAS, MICH); Levy Co., Cedar Key, Beach Park, *Zona & Geroni 90* (FLAS); Manatee Co., Madira Brickel shell mound, *Cole 100* (USF); Marion Co., N of Eureka, N of Fla 316, *Perkins & McKinney 998* (RSA); Martin Co., Jupiter Island, *Dunn 16587* (USF); Monroe Co., Cudjoe Key, *Small et al. 3576* (NY, US); Orange Co., without locality, *Fredholm 5390* (GH, MO, US); Osceola Co., Bruner's Sink, *Huck 711* (NCU); Palm Beach Co., W of Delray at junct. of Linton Blvd. and Military Trail, *Zona 159* and *160* (RSA); Pinellas Co., Dogwood Key, Ft. De Soto Park, *Thorne 48515* (RSA); Polk Co., 0.5 mi S of Withlacoochee River, 11.5 NW of Providance, *Baltzell 9746* (FLAS); Sarasota Co., 13.3 mi W of DeSoto County line on Fla 72, *Smith 340* (FLAS); Seminole Co., ca. 3 mi N of Oviedo on Fla 419, *Ray et al. 10865* (FSU, NCU, USF); Volusia Co., Tomoka State Park, *Zona 53* (FLAS); Wakulla Co., St. Mark's Wildlife Refuge, *Trott 160* (FSU).—GEORGIA: Brantley Co., 2.2 mi NE of Waynesville, *Duncan 30457* (GA); Chatham Co., Savannah Beach, 17 Oct 1964, *Hooper s.n.* (FLAS, RSA); Glynn Co., 3 mi W of Brookman, *Wiegand & Manning 666* (BH, RSA); McIntosh Co., SW of Cox along Altamaha River, *Bozeman 2707* (GA, NCU).—NORTH CAROLINA: Brunswick Co., Smith's Island, 6 Apr 1918, *Coker et al. s.n.* (NCU).—SOUTH CAROLINA: Beaufort Co., Lemon Island, SW of Beaufort on SC 170,

Fig. 27. *Sabal palmetto,* Palm Beach Co., Florida.

Boufford 15894 (MO); Charleston Co., Folly Beach, *Leonard 4357* (AUA, CM, FLAS, FSU, GA, MICH, MO, NY, RSA, USCH, USF).

Common names.—Cabbage-palm, cabbage palmetto, palmetto (USA), guana cana, guano rabo de cote, palma, palma cana (Cuba).

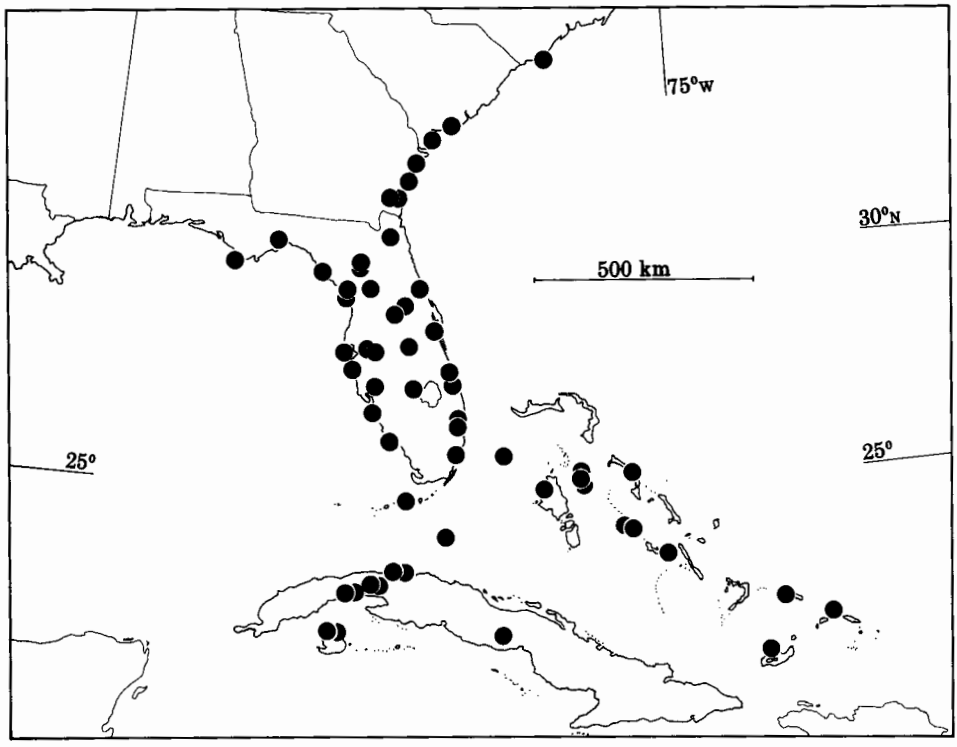

Fig. 28. Distribution of *Sabal palmetto.*

Distribution and ecology (Fig. 28).—*Sabal palmetto* is a common palm of Cuba and the Bahamas, peninsular Florida, coastal Georgia, and South Carolina; it finds its northernmost station on Cape Fear, Smiths Island, North Carolina. In the United States, it grows in mesic hammocks (with *Quercus virginiana* Mill.), pine flatwoods (associated with *Pinus elliottii* Engelm.), river banks, and dry beachside dunes and tidal flats (just above the *Juncus roemerianus* Scheele zone, in Florida). *Sabal palmetto* withstands salt spray and brackish water (Brown 1978; Zona 1983). An account of associated species may be found in Harper (1914, 1915, 1927). Brown (1973, 1978, 1982) elucidated the ecology and life history of this species. In Cuba, it is common in seasonally flooded savannas, swamps, and along water courses, as well as in disturbed vegetation. It is said to be an indicator of poor soil (Alain 1961).

In the northern portion of its range, *S. palmetto* blossoms mostly in July with little or no flowering during the remainder of the year. In central Florida, it flowers from June through August, but in southern Florida and the Bahamas, it flowers throughout the year. In Cuba, it seems to flower most abundantly in the spring.

Discussion.—When *S. parviflora* is compared with *S. palmetto,* it becomes apparent that there is little reason, other than tradition, to keep them apart. Beccari (1912) described the leaf segment apices of *S. parviflora* as very acuminate and rigid and again in 1931 described the segments as "acuminate with stiff apices." The segment apices of the Cuban palms sometimes appear rigid in the field, but

this difference is hardly reason to recognize a separate species. In fact, the leaf segments of the isotype of *S. parviflora* at NY are long, flexible, and acuminate.

Beccari (1912, 1931) used the presence of terete (when dry) rachillae in *S. florida* (=*S. maritima*) to distinguish it from *S. parviflora,* which was said to have angular rachillae. Bailey (1944) included *S. florida* (=*S. maritima*) in his circumscription of *S. parviflora* and consequently distinguished *S. parviflora* by the presence of thin, terete rachillae and narrow threadlike leaf segment apices versus irregular or angled rachillae and less attenuated apices in *S. palmetto.* The rachilla characteristic simply does not hold up in a large number of collections, not even for *S. maritima.* Another difference used by Bailey (1944), that the inflorescences of *S. parviflora* "seldom if ever" exceed the leaves, likewise is of limited usefulness and questionable validity.

The Cuban population has somewhat larger fruit and seed dimensions, but they are broadly overlapping with those of mainland *S. palmetto.* Other similarities between them are readily apparent in leaf anatomy, flavonoid chemistry, and ecology. A case might be made for recognizing the Cuban population at the infraspecific level; however, a more conservative approach is taken here.

Typification is required for *S. palmetto* and many of its synonyms. In 1927, Small described *S. jamesiana* to include an adult palm bearing juvenile foliage. He designated no types, so I have chosen as a lectotype a specimen collected by him from the type locality two years after describing the species. Bailey named two syntypes when he described *S. viatoris* in 1944. I have chosen the more complete of the two specimens as the lectotype. Likewise, I have chosen from among Becarri's three syntypes to typify *S. palmetto* var. *bahamensis*; the fertile specimen bearing Beccari's annotation is the lectotype. Walter's specimen of *Corypha palmetto* is probably no longer extant (Fernald and Schubert 1948). The neotype that I have chosen closely agrees with the protologue and is reasonably complete, and isoneotypes are widely distributed and available for study.

As circumscribed above, *S. palmetto* is a wide-ranging, weedy, and highly variable species.

12. SABAL PUMOS (Kunth) Burret, Repert. Spec. Nov. Regni Veg. 32:101. 1933. *Corypha pumos* Kunth in Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp. 1:298. 1815 [publ. 1816]. *Copernicia pumos* (Kunth) Martius, Hist. Nat. Palm. 3:319. 1853.—Type: "Mexico, mts. Jorullo, prope Villa Agua Sarco," Sep 1803, *Humboldt & Bonpland s.n.* (holotype: P, not located).

Sabal dugesii S. Watson ex Bailey, Gentes Herb. 3:335. 1934.—Type: "Rancho de Bustos, Guanajuato, Mexico," without date, *Duges s.n.* (holotype: GH!; isotype: BH!).

Slender palm to ca. 15 m tall; trunk 15–35 cm DBH, gray, smooth. Leaves 15–25, evenly green, strongly costapalmate, filiferous; petioles 1.9–3.6 cm wide and ca. 1–2 m long; hastula acute, 5–15.2 cm long, glabrous or glabrescent, margin of hastula erect and undulate or occasionally involute, flat, or revolute and entire; segments 60–80 per leaf, connate for ca. 30% of their length, middle segment 80–150 cm long, 1.8–4.0 cm wide, 0.2–0.3 mm thick, transverse commissures short and inconspicuous, apex bifurcate for 20–50 cm. Inflorescence arcuate-cernuous with 3 orders of branching, not exceeding the petioles in length, sheathing bracts glabrous or rarely glabrescent, rachillae 14–26 per branchlet, 0.7–1.1 mm in diameter, 7–14 cm long, with (5–)6–7(–8) flowers per cm. Flower 4.4–6.7 mm long;

calyx cupulate to urceolate, strongly costate when dry, 1.8–2.7 mm long, 1.5–2.1 mm wide, sinuses 0.4–1.6 mm deep; petals obovate, sparingly or noncostate when dry, membranous, 4.0–5.5 mm long, 1.8–2.5 mm wide; stamens spreading, filaments 3.7–5.3 mm long, adnate to the corolla for 1.3–1.6 mm, anthers ca. 1.8 mm long and 0.8 mm wide; gynoecium 3.4–4.6 mm long, ovary 0.7–1.4 mm high, 1.0–1.5 mm in diameter. Fruit oblate spheroidal, greenish brown-black, with a thick pericarp, 18.5–27.8 mm in diameter, 14.5–22.6 mm high; seed strongly oblate-concave, 11.8–18.8 mm in diameter, 7.5–11.2 mm high; embryo supraequatorial, rarely equatorial. (Fig. 7B, 9D, 12C.)

Representative specimens.—MEXICO. ESTADO DE MÉXICO: dist. of Temascaltepec, palmar, 650 m, *Hinton 4122* (GH, MO, NY).—GUANAJUATO: Mpio. Guanajuato, village of Cañada de Bustos, cultivated, *Zona & Tenorio 252* (RSA); same locality, cultivated, *Torres et al. 10943* (RSA).—GUERRERO: Mpio. Buenavista de Cuellar, San José Tepetlapa, at 54 km marker from Cuernavaca to Chilpancingo, *Zona et al. 174 & 175* (RSA); at km 131–132, *Moore 8113* (BH).—MICHOACÁN: Mpio. Ario de Rosales, near La Playa, *Rzedowski 22046* (MICH); Mpio. Gabriel Zamora, 5 km N of Gabriel Zamora, *Quero R. 2602* (MO); near Charapendo, *Moore et al. 5748* (BH); Mpio. La Huacana, Pedro Pablo, 6 km N of La Huacana, *Rzedowski 17307* (MICH); 3 mi N of La Huacana, *Liston et al. 631-1* (RSA); between La Huacana and La Playa, near Rancho La Agua Blanca, *Zona 250 & 251* (RSA); slopes of Jorullo Volcano, *Eggler 90* (BH); Mpio. Uruapan, above Charapendo on road from Uruapan to Apatzingán, *Moore 8148* (BH).

Common names.—Palma, palma real, pumos (fruit).

Distribution and ecology (Fig. 29).—*Sabal pumos* is endemic to the Río Balsas Basin region of the states of Michoacán, Estado de México, and Guerrero, and probably Morelos as well. Within this restricted range it is locally abundant.

The species inhabits sandy soils at the transition zone between tropical deciduous forest and oak forest at 600–1300 m (Rzedowski 1965), but much of the land in the vicinity of the type locality has been converted to pasture. Fortunately, *S. pumos* thrives in this anthropogenic habitat, and its usefulness to the local people for both fruit and thatch would seem to ensure its survival.

Herbarium records for *S. pumos* are imperfect, and reliable phenological data are not at hand. Specimens with flowers are known from March, June, October, and December (two collections). Fruits are known from March, July, August, and October. Personal observation of the species in August near the type locality revealed that out of hundreds of trees, only one had flowers and one had fruit; the remaining trees showed no signs of recent or future reproductive activity. Although flowering may be sporadic throughout the year, it probably peaks in November or December.

Discussion.—Anatomically, phytochemically, as well as morphologically, *S. pumos* is most closely allied to *S. rosei* and *S. uresana* but has the largest fruit of the three. *Sabal pumos* has many unspecialized features, which might lead one to speculate that the Balsas River Basin and the mountains of Michoacán may have served as a refugium for *Sabal,* especially for ancestral temperate species retreating from advancing Pleistocene glaciation.

13. SABAL ROSEI (Cook) Beccari, Webbia 2:83. 1907. *Inodes rosei* Cook, Bull. Torrey Bot. Club 28:534. 1901. *Sabal uresana* var. *roseana* (Cook) I. M. Johnston, Proc. Calif. Acad. Sci., ser. 4, 12:995. 1924.—Type: "Mexico, Acaponeta, State of Tepic [Nayarit]," Jul 1897, *Rose 1528* (holotype: US!; isotypes: NY! GH!).

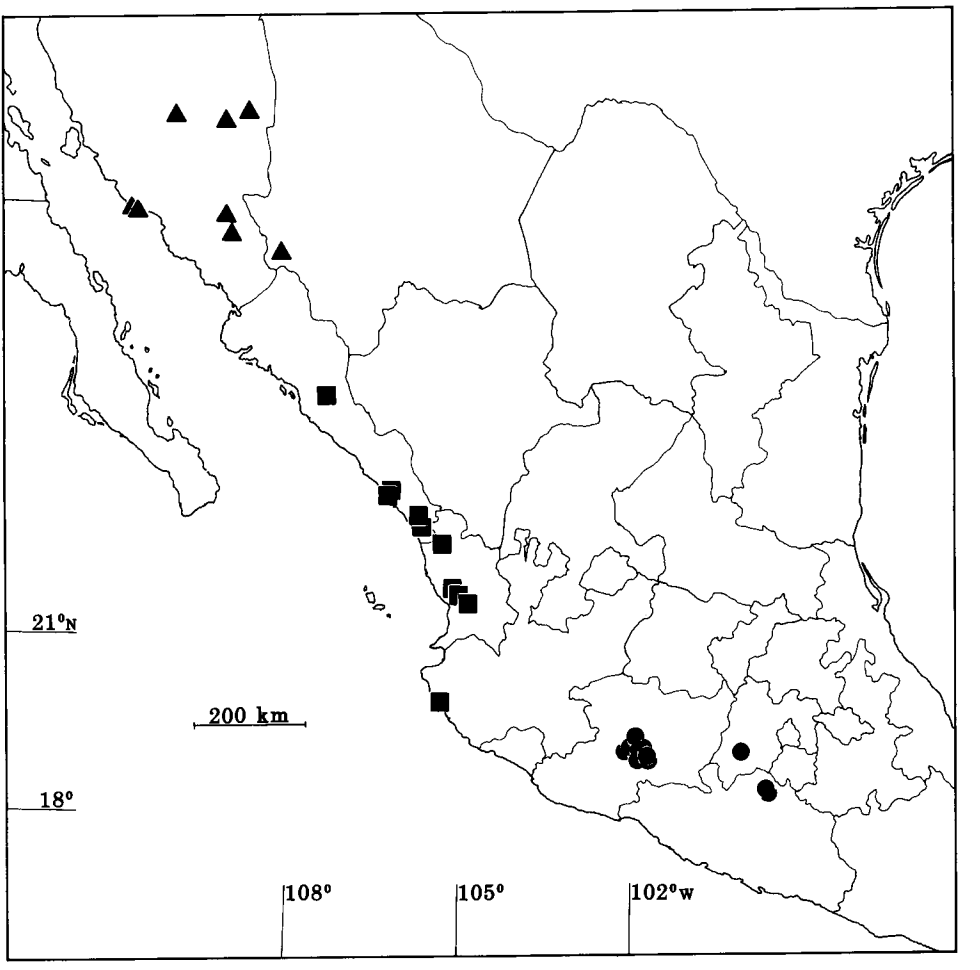

Fig. 29. Distributions of *Sabal pumos* (circles), *S. rosei* (squares), and *S. uresana* (triangles) in western Mexico.

Erythea loretensis M. E. Jones, Contr. W. Bot. 18:29. Aug 1933–Apr 1935 [publ. Aug 1933, vide Blake 1957].—Neotype, designated here: "Mexico, Baja California, at Loreto," 29 Mar 1936, *Bailey s.n.* (BH!).

Slender palm to ca. 15 m tall; trunk 15–30 cm DBH, gray, smooth. Leaves 10–30, evenly green, strongly costapalmate, filiferous; petioles 1.8–2.4 cm wide, 1–2 m long; hastula acute, 5.1–7.0 cm long, glabrescent (but often with lepidote pubescence on adaxial surface of midveins), margin of hastula flat and undulate, occasionally revolute, involute, or erect; segments 60–80 per leaf, connate for ca. 25% of their length, middle segment 55–110 cm long, 2.3–4.3 cm wide, 0.2–0.3 mm thick, transverse commissures short and inconspicuous (rarely conspicuous), apex bifurcate for 30–40 cm (rarely undivided). Inflorescence arcuate-cernuate with 3 orders of branching, equalling the leaves in length, sheathing tubular bracts glabrous, rachillae 8–23 per branchlet, 0.6–1.3 mm in diameter, 7.5–16 cm long, often curling slightly upon drying, with 5–7 flowers per cm. Flower 4.2–5.9 mm

long; calyx urceolate-cupulate, strongly costate when dry, 1.9–2.0 mm long, 1.7–1.9 mm wide, sinuses 0.5–0.8 mm deep; petals obovate, noncostate when dry, membranous, 3.7–4.8 mm long, 1.8–2.5 mm wide; stamens spreading, filaments 3.3–4.5 mm long, adnate to the corolla for ca. 1.2 mm, anthers ca. 1.6 mm long and 0.8 mm wide; gynoecium 3.3–3.8 mm long, ovary 0.9–1.1 mm high, 0.9–1.1 mm in diameter. Fruit oblate spheroidal, greenish brown-black, with a medium to thick pericarp, 15.3–22.4 mm in diameter, 13.5–20.1 mm high; seed strongly oblate concave, 10.0–15.5 mm in diameter, 6.4–8.7 mm high; embryo equatorial or supraequatorial. (Fig. 7C, 9E, 12D.)

Representative specimens.—MEXICO. JALISCO: Mpio. Tomatlán, 81 km N of Chamela toward Puerto Vallarta, *Zona et al., 248* (RSA).—NAYARIT: Mpio. Tepic, *Rose et al. 14350* (A, GH, MICH, MO); 23 km NNW of Tepic, *Quero R. 2581* (MO); Mpio. San Blas, *Zona et al. 239* (RSA); ca. 21 mi NE of San Blas, *McVaugh 12080* (MICH).—SINALOA: Mpio. Escuinapa de Hidalgo, *Gonzalez O. 5188* (GH); ca. 5 km N of Palmillas toward Escuinapa de Hidalgo, *Zona et al. 237* (RSA); Mpio. Mazatlán, N of La Cofradia, *Gentry 5221* (BH, GH, MICH, MO, NY); 7 km N of La Cofradia, *Zona et al. 236* (RSA); Mpio. Mocorito, 25 mi N of Culiacán, *Moore 6406* (BH).

Common name.—Palma de llano.

Distribution and ecology (Fig. 29).—This species is known from tropical deciduous and semideciduous forests of western Mexico. It is an abundant palm in disturbed vegetation from sea level to 600 m. Common associate species include: *Caesalpinia platyloba* S. Wats., *Casearia arguta* Kunth, *Cochlospermum vitifolium* (Willd.) Spreng., *Guazuma ulmifolia* Lam., *Hura polyandra* Baill., *Lysiloma acapulcensis* (Kunth) Benth., *Spondias purpurea* L., *Trema micrantha* (L.) Blume, and *Xylosma flexuosum* (Kunth) Hemsl., as well as species of *Acacia, Bursera, Cordia, Ficus, Tabebuia,* and *Vitex* (Rzedowski and McVaugh 1966).

Sabal rosei flowers from December to July.

Discussion.—The description of the flowers given above is based on only three specimens and may not fully describe the range of variation of floral morphology for this species.

The assignment of Jones' *Erythea loretensis* to this taxon is somewhat speculative, given the fact that Jones collected no specimen and designated no type (Blake 1957). The photograph published by Jones is unquestionably of a *Sabal,* but the broad range of fruit size given by Jones for his species could accommodate either *S. uresana* or *S. rosei.* In Jones' key to *Erythea,* the leaves of *E. loretensis* are described as green (as in *S. rosei*), not glaucous as in *S. uresana.* For these reasons, *E. loretensis* is assigned to *S. rosei,* and Bailey's topotype specimen, collected only three years after Jones' publication, is chosen here as a neotype.

Sabal rosei clearly shares a common ancestry with the two other western Mexican species, *S. pumos* and *S. uresana.* Of the three, *S. rosei* is the most widespread.

14. SABAL URESANA Trelease, Annual Rep. Missouri Bot. Gard. 12:79. 1901. *Inodes uresana* (Trelease) Cook, Bull. Torrey Bot. Club 28:534. 1901.—Type: "Mexico, Sonora, in the uplands, a few miles north of Ures," 17 Aug 1900, *Trelease s.n.* (holotype: MO!, photo: RSA!).

Large palm to ca. 20 m tall; trunk 30–40 cm DBH, smooth and gray-brown. Leaves 15–35, moderately to highly glaucous, especially on the abaxial surface, strongly costapalmate, filiferous or not; petiole ca. 3.5 cm wide and 1–2 m long;

hastula acute, ca. 17 cm long, glabrous, hastula margin erect or involute, entire; segments 60–75 per leaf, connate for ca. 35% of their length, middle segment 105–110 cm long, 3.3–4.4 cm wide, 0.3–0.5 mm thick, transverse commissures inconspicuous, apex bifurcate for 38–61 cm. Inflorescence arcuate with 3 orders of branching, equalling the leaves in length, sheathing tubular bracts glabrous, rachillae 16–21 per branchlet, ca. 0.9 mm in diameter, 5–12 cm long, with ca. 16 flowers per cm. Flower (based on 5 flowers from *Johnston 4345*) 4.4–5.3 mm long; calyx cupulate-urceolate, strongly costate when dry, 1.5–1.9 mm long, 1.4–1.6 mm wide, sinuses 0.4–0.9 mm deep; petals obovate, noncostate when dry, membranous, 3.4–3.8 mm long, 1.4–2.1 mm wide; stamens spreading, filaments 3.6–4.5 mm long, adnate to the corolla for 0.5–0.8, anthers ca. 1.5 mm long and 0.8 mm wide; gynoecium 2.9–3.4 mm long, ovary ca. 0.9 mm high, ca. 1.0 mm in diameter. Fruit oblate-spheroidal to oblate-pyriform, brown-black, 13.5–18.4 mm in diameter, 10.7–14.5 mm high; seed oblate concave, 9.7–14.1 mm in diameter, 6.0–7.8 mm high; embryo supraequatorial. (Fig. 7D, 9F, 13A, 30.)

Representative specimens.—MEXICO. CHIHUAHUA: Mpio. Guazapares, Barranca Cobre, near Fuerte and Chinapas Rivers, 1939, *Lindsay s.n.* (BH).—SONORA: Mpio. Guaymas, San Carlos Bay, *Johnston 4345* (A, GH, NY); same locality, *Zona et al. 257*; Mpio. Hermosillo, cultivated, *Rose et al. 12518* (A, GH, MO, NY); principal plaza of Hermosillo, cultivated, *Rose et al. 12519* (GH, NY); Mpio. Nacori Chico, Río Bonito, *Muller 3644* (GH); Mpio. Quiriego, between Quiriego and San Bernardo, *Zona et al. 260* (RSA); Mpio. Rosario, 6–10 mi S of Las Movas along western road to El Sauz, *Zona et al. 263* (RSA); Mpio. Tepache, 7.7 mi SW of Tepache, *Carter et al. 71-53* (BH).

Common names.—Palma, palma blanca, palma de sombrero, Sonora palmetto, tahcu (Gentry 1942).

Distribution and ecology (Fig. 29).—*Sabal uresana* occurs in thorn forest and oak forest along watercourses and valleys in the foothills of the Sierra Madre Occidental in Sonora and Chihuahua, Mexico. It can be found from sea level to 1500 m, with most populations found above 650 m (Gentry 1942). Associated species include *Acacia cochliacantha* Humb. & Bonpl. ex Willd., *A. pennatula* (Schl. & Cham.) Benth., *Conzattia sericea* Standl., *Guazuma ulmifolia* Lam., *Jacquinia pungens* A. Gray, *Lycium exsertum* A. Gray, *Prosopis juliflora* (Sw.) DC., and *Quercus chihuahuensis* Trel. A complete account of the vegetation of the region can be found in Gentry (1942).

Sabal uresana apparently flowers in mid-summer, but phenological records are scanty.

Discussion.—Herbarium records of *S. uresana* are poor. Precious little flowering material is available, and many collections in North American herbaria represent sterile seedlings. Consequently, the above description does not reflect the full range of variation found within this species.

Populations of *S. uresana* are not abundant and are never large. Gentry (1942) stated that the species was declining in abundance and assigned cause variously to drought, over-exploitation by the indigenous people, and bruchid beetle predation upon seeds. Historical records are not sufficient to document its decline, although its present rarity stands in stark contrast to the abundant stands of *S. rosei* to the south. If populations of *S. uresana* are dwindling, over-exploitation for timber, thatch, and fiber is probably the reason.

Fig. 30. *Sabal uresana,* Mpio. Quiriego, Sonora, Mexico.

15. SABAL YAPA Wright ex Beccari, Webbia 2:64. 1907. *Inodes japa* (Becc.) Standley, Contr. U.S. Nat. Herb. 23:71. 1920.—Type: "Cuba," without date, *Wright, 3971* (holotype: B [destroyed], fragment?: FI!; isotypes: A! NY! P! US!).

Sabal mayarum Bartlett, Publ. Carnegie Inst. Wash. 461:35. 1935.—Type: "British Honduras, Maskall," 19 Feb 1934, *Gentle 1156* (holotype: MICH!; isotypes: GH! MO! NY!).

Sabal peregrina Bailey, Gentes Herb. 6:400. 1944.—Type: "Florida, cultivated Key West," 5–7 Aug 1935, *Bailey 322X* (holotype: BH!).

Sabal yucatanica Bailey, Gentes Herb. 6:418. 1944.—Type: "Mexico, Yucatán, Chichen Itza in yard of hacienda," Jun–Jul 1938, *Lundell & Lundell 7368* (holotype: MICH!, fragment: BH!).

Slender palm to ca. 20 m tall; trunk 15–26 cm DBH, green and prominently ringed when young and aging to brown-gray. Leaves 15–20, evenly green, moderately costapalmate, not filiferous; petiole 2.3–3.5 cm wide, ca. 0.5–2 m long; hastula acuminate, 4.8–6.7 cm long, glabrescent (or lepidote on the abaxial side of midveins at their insertion to the petiole), margin of hastula revolute, erect, or involute, undulate; segments 90–115 per leaf, connate in groups of 2 (rarely 3) for ca. 50% of their length, the groups connate for only ca. 15% of their length, middle segment 90–125 cm long, 2.0–3.2 cm wide, 0.1–0.2 mm thick, transverse commissures abundant, long, and conspicuous, apex bifurcate for 9–23 cm. Inflorescence ascending (sometimes becoming arcuate in fruit) with 3 orders of branching, exceeding the leaves in length, sheathing bracts lepidote or glabrescent, rachillae 6–28 per branchlet, 0.5–1.3 mm in diameter, 4–10 cm long, with (6–)8–9(–10) flowers per cm. Flower 4.0–5.7 mm long; calyx strongly campanulate, shriveled but not costate when dry, 1.5–2.3 mm long, 1.5–2.7 mm wide, sinuses 0.2–1.2 mm deep; petals triangular-ovate, noncostate when dry (rarely weakly costate), carnose, basally connate, reflexed at anthesis, 3.3–4.4 mm long, 2.2–2.8 mm wide; antipetalous stamens reflexed, antisepalous stamens erect-ascending, filaments acuminate, 2.6–4.6 mm long, basally connate and adnate to the corolla tube for 0.8–2.0 mm, anthers ca. 1.8 mm long and 0.9 mm wide; gynoecium 2.7–5.0 mm long, ovary 0.5–1.9 mm high, 0.9–1.9 mm in diameter. Fruit spheroidal to pyriform, blackish, 9.8–12.8 mm in diameter, 8.9–12.2 mm high; seed oblate spheroidal, 6.1–8.9 mm in diameter, 4.7–5.5 mm high, usually with smooth funicular remains; embryo supraequatorial, rarely equatorial. (Fig. 4A, 7E, 9G, 13B.)

Representative specimens.—BELIZE. COROZAL Dist.: *Gentle 602* (MICH), *Gentle 628* (MICH).—CUBA. Without locality, *Sagra 222* (FI).—ISLA DE LA JUVENTUD (Isle of Pines): without locality, *Britton et al. 14646* (CM, GH).—LA HABANA: Mpio. Batabanó, W of Batabanó, Peralta, *León 14287* (GH), *León 13908* (GH), *Marie-Victorin 58168* (GH); Monte de Qunitana, *León 14160* (BH); Mpio. La Habana, Santiago de las Vegas, near La Peta, 21 Mar 1931, *Roig & Van Hermann s.n.* (BH).—PINAR DEL RÍO: Boquerón, *Bailey 15183* (BH); Mpio. San Juan y Martínez, hillside near Galafre, *Britton & Cowell 9845* (GH, MO).—MEXICO. CAMPECHE: Mpio. Ciudad del Carmen, between Sabancuy (and Checobul) and intersection with Hwy. 186, *Zona et al. 146* (RSA); Rancho el Zaiz, ca. km 183 on Villahermosa-Escárcega Hwy., *Quero R. 2387* (MO); Mpio. Tenabo, along Campeche-Tenabo Hwy. (24), 37 km from Campeche, *Zona et al. 143* (RSA).—QUINTANA ROO: Mpio. Cozumel, Coba, bordering Lake Macanxoc, *Lundell 7727 & Lundell* (MICH); Mpio. Morelos, Chichankanab, *Gaumer 1359* (GH, MO).—YUCATÁN: without locality, *Gaumer 317* (FI, MO, NY), *Gaumer 24166* (A, MO, NY); Mpio. Halacho, Halacho, *Quero 2327* (MO); Mpio. Izamal, Izamal, *Gaumer et al. 23316* (A, GH, MO, NY); Mpio. Maxcanu, Maxcanu, in Mayan garden, *Zona et al. 144* (RSA).

Common names.—Bay, thatch palm (Belize), botan (Belize and Guatemala); cana, cana japa, chagareta, guano blanco, miraguano, palma cana, palma cana del monte, palma guano (Cuba), guano bonshan, jul-ook xa'an (Mexico).

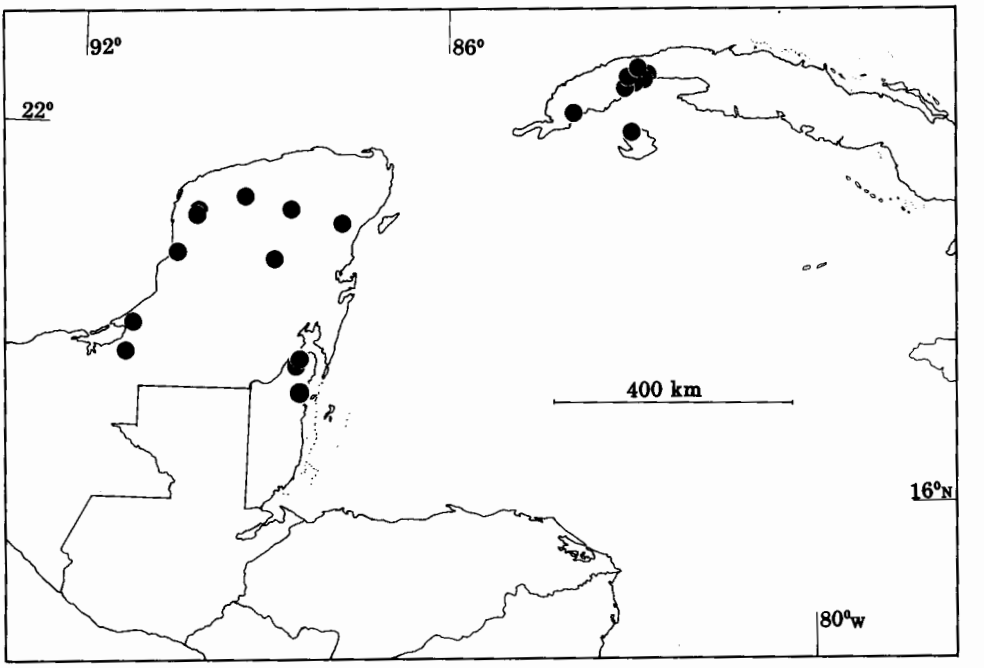

Fig. 31. Distribution of *Sabal yapa.*

Distribution and ecology (Fig. 31).—*Sabal yapa* is widespread in the Yucatan Peninsula from sea level to 100 m on well-drained, limestone soils, often on the steep banks of swamps or sinkholes (Lundell 1937). It grows in upland forests associated with *Manilkara zapota* (L.) Van Royen, *Brosimum alicastrum* Swartz, *Callophyllum brasiliense* Camb. var. *rekoi* Standl., *Lucuma campechiana* Kunth, and *Swietenia macrophylla* King (Bartlett 1935; Lundell 1937). In Cuba, it is found on both swampy and dry soils, also on limestone. It persists after forests are cleared and burned for agricultural use.

In Yucatán, *Sabal yapa* grows sympatrically with *S. mexicana,* a species probably introduced to the peninusula by pre-Columbian peoples. In Cuba, *S. yapa* can be found growing with *S. palmetto* and *S. maritima* in Batabanó.

Sabal yapa flowers in the first half of the year (January–July) with sporadic flowering at other times.

Discussion.—This species is the most specialized in the genus. Several floral characteristics are unique to *S. yapa,* including campanulate calyx, ovate petals without hyaline margins, and basally connate petals. It also shares a number of derived features with *S. mauritiiformis,* such as overall growth habit, leaf venation and texture, and clustered leaf segments. Anatomical features suggest, however, that *S. yapa* is more drought-adapted than *S. mauritiiformis,* and thus, the two are probably ecologically separated.

EXCLUDED NAMES AND NOMINA NUDA

The following list of names does not include herbarium names that were never published, nor does it include those names appearing in Moore (1963) that were

not accepted by him but for which no other authorities have been established. In both cases, the names have no validity and must not be used. For this reason, they are not repeated here.

Inodes vestita Cook, Bull. Torrey Bot. Club 28:533. 1901, nomen ambiguum. [No types exist of this species, described from a juvenile plant cultivated in New York. Cook's description is not sufficient to establish with certainty the identity of this taxon.]

Sabal acaulis J. Blanchard, Revue Hort. 1885:414. 1885, nomen nudum.

S. adansonii Guersent var. *major* H. Wendland, Ind. Palm. 35. 1854, nomen nudum.

S. australis hort. ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 42. 1892, nomen nudum. [This name, along with several other garden names, appears in Pfister's 1892 anatomical study of coryphoid palms. Validly published and unpublished garden names (nomina nuda) were used indescriminately. Pfister's work was not meant to be a taxonomic monograph of the palms (only a few of the known species were studied) nor were any nomenclatural changes proposed (even when anatomical similarities were noted among some entities). In many cases, Pfister mentioned different entities (with different anatomical features) bearing the same name but originating from different botanical gardens. Although entities are described anatomically, Pfister had no intention of describing new species, so in accordance with Art. 34.3 of the ICBN, none of Pfister's names can be recognized as validly published.]

S. blackburnia Glazebrook, Gard. Mag. & Reg. Rural Domest. Improv. 5:52. 1829, provisional name.

S. blackburniana Glazebrook ex J. A. & J. H. Schultes, Syst. veg. 7:1488. 1830, 'blackburnianum,' nomen ambiguum. ["The confusion regarding this palm is almost endless." (Hemsley 1885, p. 73). See discussion after description of *Sabal bermudana* Bailey.]

S. carat Lefroy, Bot. Bermuda, Bull. U.S. Nat. Mus. 25:113. 1884, nomen nudum.

S. caroliniana hort. ex Poiret in Lamarck, Encycl. 6:356. 1804, nomen nudum.

S. chinensis hort. ex Beccari, Ann. Roy. Bot. Gard. (Calcutta) 13:297. 1931, nomen nudum, pro syn. *S. adansonii* Guers. [Not accepted by Beccari.]

S. coerulescens hort., Kew Rep. 1882:63. 1884, nomen nudum.

S. columnaris Loddiges ex Martius, Hist. nat. palm. 3:320. 1853, nomen nudum.

S. dealbata hort. ex Bailey, Stand. Cycl. Hort. 6:3045. 1917, nomen nudum.

S. denisoni hort. ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 41. 1892, nomen nudum. [See above remarks under *S. australis*.]

S. elata Loddiges ex Martius, Hist. nat. palm. 3:320. 1853, nomen nudum.

S. excelsa D. Morris, Colony of Brit. Honduras 68. 1883, nomen nudum.

S. extonianum hort. ex Gentil, Pl. Cult. Serres Chaudes Jard. Bot. Brux. 170. 1907, nomen nudum.

S. filamentosa H. Wendland ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 42. 1892, nomen nudum. [See above remarks under *S. australis*.]

S. filifera hort. ex André, Illus. Hort. 24:107. 1877, nomen nudum, pro syn. *Pritchardia filifera* Linden [=*Washingtonia filifera* (Lind.) H. Wendland].

S. floribunda Katzenstein, Cat. 1934, nomen nudum.

S. ghiesebrechtii hort. ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 41. 1892, nomen

nudum. [As "ghiesbrechtii" in Kew Ind. and "giesbreghtii" in Beccari 1907); see above remarks under *S. australis.*]

S. giganteum Fulchiron ex J. A. & J. H. Schultes, Syst. veg. 7:1488. 1830, nomen nudum, pro syn. *S. blackburniania* Glazebrook ex J. A. & J. H. Schultes.

S. glabra (Miller) Sargent, Silva 10:38. 1896, nomen ambiguum. [This name is based on Miller's 1768 description of *Chamaerops glabra* in Gardener's Dictionary, 9th ed. Sargent believed this to be an earlier epithet for *Sabal minor.* Miller described a palm with an underground trunk, unarmed petioles, and palmate leaves. He discussed the possibility that *C. glabra* may be the same as the "Carolina Palm," seeds of which he received from North America; the Carolina palm is undoubtedly *Sabal minor.* Miller's description contains two important details which argue against its application to *S. minor*: *C. glabra* was described as androdioecious with only imperfectly formed male flowers having been produced under cultivation in England, and it was said to have come from Jamaica. Three genera of fan palms are known from Jamaica: *Thrinax, Coccothrinax,* and *Sabal,* all of which are hermaphroditic and arborescent. Since Miller's description is insufficient, the name must be treated as a nomen ambiguum.]

S. glauca hort. ex Bailey, Std. Cycl. Hort. 6:3045. 1917, nomen nudum.

S. gluestrightii Eichhorn, Rev. Cytol. Biol. Vég. 18:148, nomen nudum. [Also given as "gluestreghtii," p. 150.]

S. graminifolia Loddiges ex J. A. & J. H. Schultes, Syst. veg. 7:1488. 1830, nomen nudum.

S. havanensis Loddiges ex Martius, Hist. nat. palm. 3:320. 1853, nomen nudum.

S. henekenii Martius, Hist. nat. palm. 3:167. 1838, nomen nudum.

S. hoogendorpii hort. ex Bailey, Stand. Cycl. Hort. 6:3045. 1917, nomen nudum, pro syn. *Livistona hoogendorpii* Teysmann & Binnendijk ex F. A. W. Miquel.

S. hystrix (Pursh) Nuttall, Gen. 1:230. 1818, 'histrix' = *Rhapidophyllum hystrix* (Pursh) H. Wendland & Drude.

S. ? japa Sauvalle, Anales Acad. Ci. Méd. Habana, 8:562. 1870, nomen nudum.

S. javanica hort. ex Bailey, Stand. Cycl. Hort. 6:3045. 1917, nomen nudum, pro syn. *S. havanensis* Loddiges ex Martius.

S. longipedunculata hort. ex Gentil, Pl. Cult. Serres Chaudes Jard. Bot. Brux. 170. 1907, nomen nudum.

S. longifolia hort. ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 42. 1892, nomen nudum. [See above remarks under *S. australis.*]

S. magdalenae Linden, Illust. Hort. 28:32. 1831, nomen nudum.

S. magdalenica Wallis ex Regel, Gartenfl. 29:230, t. 1022. 1880, nomen nudum.

S. megacarpa hort. ex Beccari, Webbia 2:19, 1907, nomen nudum, non *S. megacarpa* (Chapman) Small. [Not accepted by Beccari.]

S. mexicana Sauvalle, Fl. Cubana, 152. 1873, nomen nudum.

S. mocini hort. ex Siebert & Voss, Vilmorin's Blumengar., ed. 3, 1:1146. 1895, nomen nudum, pro syn. *Sabal palmetto* (Walter) Loddiges ex J. A. & J. H. Schultes.

S. mocini hort. ex H. Wendland, Index palm. 35. 1854, nomen nudum, pro syn. *S. mexicana* Martius et *S. minima* Nuttall.

S. morrisiana Bartlett, Carnegie Inst. Washington Publ. 461:17. 1935, nomen nudum.

S. nitida Dahlgren, Field Mus. Nat. Hist., Bot. Ser. 14:252. 1936, nomen nudum. [Not accepted by Dahlgren. In misreading H. Wendland's list of accepted names published in Kerchove's Les Palmiers, Dahlgren created this nomen nudum.]

S. oleracea Loddiges ex Martius, His. nat. palm. 3:320. 1853, nomen nudum.

S. palmetto Rein, Ber. Senckenberg. Naturf. Ges. Frankfurt 1873: 150. 1873, nomen illeg., non *S. palmetto* (Walter) Loddiges ex J. A. & J. H. Schultes, 1830.

S. picta hort. ex H. Wendland, Index palm. 35, 36. 1854, nomen nudum, pro syn. *S. havanensis* Loddiges ex Martius et *S. palmetto* (Walter) Loddiges ex J. A. & J. H. Schultes.

S. princeps hort. ex H. Wendland in Kerchove, Palm. 356. 1878, nomen nudum. [Not accepted by Wendland.]

S. rubrum H. Cels. ex J. A. & J. H. Schultes, Syst. veg. 7:1488. 1830, nomen nudum.

S. sanfordii Linden, Illust. Hort. 28:32. 1831, nomen nudum.

S. serrulata (Michaux) Nuttall ex J. A. & J. H. Schultes, Syst. veg. 7:1486. 1830. =*Serenoa repens* (Bartram) Small.

S. serrulata var. *minima* (Nuttall) Wood, Class-book 667. 1861. =*Serenoa repens* (Bartram) Small.

S. speciosa hort. ex Ricasoli, Giard. d'acclimaz. 77. 1888, nomen nudum.

S. spectabilis hort. ex Pfister, Beitr. vergl. Anat. Sabaleenbl. 41. 1892, nomen nudum. [See above remarks under *S. australis*.]

S. taurina Loddiges ex Martius, Hist. nat. palm. 3:320. 1853, nomen nudum.

S. tectorum hort. ex Ricasoli, Giard. d'acclimaz. 77. 1888, nomen nudum.

S. umbraculifera Martius, Hist. nat. palm. 3:245. 1839, nomen ambiguum. [This name has been a persistent cause of confusion. Martius based his description of the fruits on material he had not seen and from a different collection (and species?). The description and plates are not sufficient to identify the species; the characters cited by Bailey (1939), i.e., undulate penultimate inflorescence branches and acuminate tubular bracts, are of no value in fixing the identity of this species. Martius applied the name to plants from Cuba, Hispaniola, Bermuda, Bahamas, etc., as well as to cultivated plants. Later authors applied this name to *Sabal* from Mexico, Hispaniola, Bermuda, Cuba, Jamaica, and Puerto Rico. This name is best rejected in accordance with ICBN Art. 69.]

S. umbraculifera Reade, Pl. Bermudas 81. 1885, nomen illeg., non *S. umbraculifera* Martius, 1839.

S. woodfordii Loddiges ex Martius, Hist. nat. palm. 3:320. 1853, nomen nudum.

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APPENDIX 1. VOUCHER SPECIMENS FOR ANATOMICAL AND PHYTOCHEMICAL STUDIES

Sabal bermudana: *Bailey 73*[1] and *397,*[1] Huntington Bot. Garden acc. 30266,[2] Kew acc. 486-33-48601,[1] *Zona 283,*[3] *284,* and *289.*[1]

S. causiarum: *Bailey 18*[1] and *43,*[1] *D'Arcy 4950,*[1] Huntington Bot. Garden s.n.,[2,3] *Questel 468,*[1] *Zona et al. 290* and *293.*

S. domingensis: *Bailey 238,*[1] Fairchild Trop. Garden acc. 63-85,[3] *Jacquemont s.n.*[1]

[1] Used only for anatomical studies. [2] Used only for phytochemical studies. [3] Examined for negatively charged flavonoids.

S. etonia: *Thorne & Judd 57944*,[1] *Perkins 997*,[2] *Zona s.n.*,[2,3] *14*,[1] and *116*.[1]
S. guatemalensis: *Moore 8209*.[1]
S. maritima: *Bailey 15158*,[1] *Bonpland 1355*,[1] *Combs 292*,[1] *Harris 9736*,[1] *León 13394*,[1] *Zona 279, 298*,[3] *299*, and *301*.
S. mauritiiformis: *Allen 2604*,[1] *Bailey 19*,[1] *Henderson et al. 723*,[1] *Zona et al. 141*,[3] *264*, and *295*.
S. mexicana: *Bomhard s.n.*,[1] *Zona 138*,[3] *139*,[2] *140*,[1] and *221*.[1]
S. miamiensis: *Small & Nash s.n.*[1]
S. minor: Huntington Bot. Garden s.n.,[2] *Lakela et al. 26375*,[1] *Perkins & Herring 987*.[3]
S. palmetto: Huntington Bot. Garden 31680,[2,3] *Wright 3970*,[1] *Zona 158, 159*,[3] *160*,[1] *221*,[1] and *280*.[3]
S. pumos: *Liston et al. 631-1, Torres et al. 10943, Zona & Tenorio 252*,[1] *Zona et al. 174*,[1] *Zona 250*, and *251*.[3]
S. rosei: *Gentry 5221*,[1] Huntington Bot. Garden acc. 17761[2] and 22632,[2,3] *Zona et al. 236*,[2] *240*, and *248*.[1]
S. uresana: *Zona et al. 257, 256*,[1] and *263*.[2,3]
S. yapa: *Bailey 12564*,[1] *Zona et al. 143*,[3] *144*, and *146*.[2]
Brahea dulcis: *Zona et al. 249*.[3]
Washingtonia filifera: *Zona 162*[1] and *165*.[2,3]